# STUDIES ON
# PLUMAGE IN THE MALE BROWN LEGHORN FOWL

by

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## 1. The Sequence of Plumage Types from Hatching to Maturity.

### Introduction

In recent years intensive investigations on the plumage dimorphism characteristically developed in most breeds of domestic fowl have resulted in a great increase in our knowledge concerning the role of the endocrine glands, in particular the thyroid and the sex organs, in relation to plumage differences. Since however, the majority of these researches have been directed to the plumage exhibited by the adult bird it is suggested that an analysis, both observational and experimental, of the earlier plumage phases shown successively from hatching to maturity might yield much valuable data concerning the nature of the hormonic stimuli /

stimuli involved.

The morphology of the specific plumage types appearing between hatching and maturity in the male of the Brown Leghorn breed of fowl have already been described to some extent, (Domm, '27, Greenwood and Blyth, '29, Juhn, Gustavson and Gallagher, '32), but a detailed analysis of such aspects of the general problem as (1) the determination of the age at which the specific plumage types make their appearance and (2) whether or not the conditioning mechanism exerts its effect on all regions of the body simultaneously, remain to be investigated.

Material.

All the birds used in this and subsequent investigations were derived from the pure-bred Brown Leghorn stock which has been maintained at /

at this Institute for a number of years. For the observational studies on plumage development in the male, chickens, hatched on the same day, were kept under identical conditions as regards husbandry. Of the original group of one day-old chicks, selected before the sexes could be determined from the external characters, 5 were subsequently found to be males and form the material on which this analysis is based.

From the time of hatching observations were made every alternate day until the birds were 3 months old. From then on they were examined twice weekly until they reached the age of four and one half months, and subsequently once a week until they were mature.

(1) The Down Plumage.

The down is the primary feather type developed by the chick and begins to appear on the /

the embryo about the 10th day of incubation; at hatching it forms a complete covering. While structural differences in the down from the various body regions are not evident there is developed a characteristic pattern due to colour differentiation (Plate 1). A wide deep brown band extends along the dorsal surface from the crown of the head to, and including, the pygostyle. In the neck region and posteriorly the colour tends to be diluted, but elsewhere along the back there is an intensification of the brown pigment especially noticeable at the margin of this colour band. The broad medial band is enclosed by two longitudinal light brown stripes which are bounded laterally by dark brown down. The intensity of pigmentation decreases passing towards the ventral region and ultimately becomes yellow on the abdomen.

Characteristically /

Characteristically there is a short strip of dark brown down starting posteriorly to the eye and extending anteriorly, bifurcating into branches running along the upper and lower eyelid respectively.

The wings are uniformly covered with medium brown down and at their posterior margin a few infantile, dark coloured, definite flight feathers are found.

Individual differences with regard to the intensification of the colour , but not the distribution, are frequently met with.

(2) Chick Plumage.

The down forms the main covering of the chick for some time but is subsequently replaced by definitive feathers. Although these begin to appear within a comparatively short time after hatching, complete replacement of the down may be long delayed and it can still be identified /

identified even well into the juvenile state. This is due to the fact that the appearance of the definitive feathers does not occur simultaneously on all regions of the body.

(a) Order of Feathering by Regions.

By the second day after hatching seven or eight wing primaries and secondaries, and their coverts had emerged. (Plate 2). On the third day some feathers appeared on the tail, (rectrices) and shoulder, (Plate 3). Thereafter an increase in the number of feathers developing in these regions took place and by the 8th day new foci of feather growth were visible on the hallux and wing bow area, (Plate 4). Growth of the definitive feathers was rapid, especially the rectrices and remiges. Breast and thigh feathers began to emerge about the 13th day, the former slightly in advance of the latter. There was no marked difference in time of emergence of the /

the anterior and posterior regions of the breast. Feathering on the neck appeared next and by the 15th day a row of minute feathers was added to the frontal adge of the wing. (Plate 5). Back feathers emerged at about the 17th day. By the 21st day a line of feathers running along either side of the sternum to the extreme posterior end of the body had made their appearance (Plate 6). Up to this time the number of feathers in the other areas have been increasing rapidly in number and the chick plumage is now complete. The cape region has not yet been differentiated.

(b) Order of Feathering within Regions.

Besides the orderly fashion in which feathers first appear in the various regions of the body there is a further definite seriation of emergence within these areas. A diagrammatic representation of the process, constructed from observational /

observational data from the individual birds, is shown in Plate 6. This sequence, determined for the first definitive plumage, reappears subsequently when the juvenile plumage is assumed and may possibly obtain in the adult as well. In Plate 6 the larger dots indicate the initiation of feathering and the extension follows the direction of the arrows; thus the order on the wing is usually in a disto-proximal direction except that the wing primaries and primary coverts appear in the reverse direction. The sequence on the shoulder is a postero-anterior one. The order of emergence in the wing primaries, secondaries and rectrices is indicated numerically; since a number of these feathers are already present at hatching this order is not completely established until replacement by the adult form takes place.

Foci of feather growth appeared on the anterior /

anterior and posterior breast almost simultaneously and approached each other eventually forming a narrow tract; at the same time the anterior group extended forward along the ventral aspect of the neck. When the tract was completed in length new feathers were added laterally on both sides.

Originally the neck hackles form two parallel lines of growing feathers on the dorsal surface, extending forwards from the base of the neck, but before reaching the occipital region they multiply in number increasing the width of the tract. While numerous minute feathers at the anterior end of this tract are spreading over the frontal head region a posterior extension appears and it is from the latter that the future cape feathering ultimately develops.

Thigh feathering appeared first as two obliquely imbricated rows to which feathers were added at both ends up to a maximum of twelve. New rows /

rows were added anteriorly until five or six were completed. At a later stage the meeting of these with adjoining feather tracts gives the thigh feathers an appearance of arrangement at random.

Back feathering in the chick appears along the mid-dorsal line at the caudal end and extends anteriorly but ceases a considerable distance short of the neck tract. No further extension was found to occur for several weeks. Multiplication of feathers laterally caused a widening of the tract but never beyond the limit formed by the crescent of the innominate bone at its widest part.

Feathers of the lateral thoracic wall do not arise from the breast tract by lateral extension but form a special area by themselves.

Other pterylae, such as those found on the abdomen and legs also show a definite feathering /

feathering order, but as their sexual character is less well marked they have not been considered in detail.

(c) Regional Morphology of Feathers.

By the age of five weeks all the regions under consideration were well plumed with definitive contour feathers except the thigh where semiplumes were exhibited. In the various areas feathers were obviously different in size, shape and pattern but there was no sharp difference in colouration although the mode of pigment distribution varied considerably.

Wing and Shoulder Feathers:

The primaries are relatively long, curved, bluntly tipped and asymetrical in shape due to the outer web being far narrower than the inner portion of the vane. They are pure black in colour apart from an occasional fine mottling of buff on the outer web.

The /

The primary coverts and thumb feathers only differ from the primaries in their smaller size.

Secondaries resemble the primaries in structure but show differences in pigmentation; the inner web of the feathers is invariably black with a stippled point while the outer is drab with fine black mottling. Transverse bars of black on the outer web, caused by concentration of pigment, are frequently met with. The drab colour deepens to brown towards the proximal end of the feathers with a corresponding decrease in the amount of black pigment. In both primaries and secondaries the proximal fluff or downy portion of the feather is much reduced.

In structure and colour the secondary coverts are a smaller edition of the secondaries, but there is no loss of melanin in the proximal part of the feathers.

Wing /

Wing bow and shoulder feathers in the chick are alike in pattern and colouration, (Plate 7, fig. 1, Plate 7, fig. 6); the lower third of the vane is almost black while the distal portion is drab, roughly barred with melanin. The proximal end of the feathers is downy and greyish in colour. There are slight structural differences between the feathers from these two regions in that shoulder feathers are larger and have a rounded tip whereas the end of the wing bow feather is blunt and rather square.

Tail Feathers:

The main tail feathers are long and blunt with a small proximal portion of fluff; sometimes the lower half of the feather is pure black while the upper part is a mixture of black and drab.

Breast Feathers:

Feathers from the anterior region of the breast /

breast are mainly salmon coloured at the tip. This pigment extends down the shaft, and involves the adjacent part of the vane, for half the total feather length. (Plate 8, fig. 11). The remainder of the vane is dark grey and this grey pigmentation always protrudes into the apical region in the form of stippling. The lower half of the feather is fluffy and of a whitish colour and here the barbs are loosely arranged due to the poor development of hooklets on the barbules. In shape the feathers are broad with a rounded apex.

The posterior breast feathers (Plate 8, fig. 15) are intermediate in structure between contour and semiplume form with a stout rhachis along which the downy barbs are situated; the loose fluffy texture is due to the lack or poor development of hooklets. Compared with the anterior /

anterior breast feathers they are longer and more darkly pigmented.

Thigh Feathers :

The thigh feathers are typical semiplumes; they are somewhat alike in colour and structure to those of the posterior breast, but whereas the barbules on feathers from the latter region are well formed those on the thigh feathers are rather defective (Plate 8, fig. 17).

Neck Feathers:

Chick neck hackles are short, broad feathers with poorly developed barbules giving the feather a slack appearance. The lateral edges and a narrow central strip are yellow in colour while a broad black band runs up each vane half finally fusing over the rhachis at the distal end. (Plate 9, fig. 19).

Back and Saddle Feathers:

Feathers in these regions are all alike at this stage, being short, blunt and greyish black./

black. They are intermediate in structure between contour feathers and semiplumes having rounded tips but loose, hookless barbules. The vane and the fluff merge into one another without any clear line of demarcation. (Plate 9, fig. 22).

(d). <u>Summary of Observations on Chick Plumage.</u>

The first appearance of definitive plumage in the different regions of the body occurs in a constant sequence. Within these regions a definite order of feather emergence also obtains. This seriation is not peculiar to the chick but reappears in the juvenile stage; it may also occur in the adult.

Two pigments are characteristic of the chick plumage, drab and black; the latter predominates even in regions with least melanic pigment such as the anterior breast. The red colouration /

colouration typically found in the feathers of both juvenile and adult males is never present at this stage.

Chick feathers are characterised by a full development of barbules along the barbs, except in those of the thigh where semiplumes are present.

(3) Juvenile Plumage.

The juvenile phase in the plumage has been arbitrarily defined to include all feather types between the chick plumage and the adult form. It begins with the first indications of sexual dimorphism and its characteristic features are the appearance of red pigment, the exhibition of a free, barbuleless border on the distal margin of many feather vanes, and the definition of distinctive feather types on various regions of the body.

Since these new phenomena may be taken as /

as a reflection of changing physiological conditions there is no reason to expect a sharp line of demarcation between the chick and subsequent feather types and indeed it has been observed that juvenile characters first appear on feathers in the process of growth.

At the time of completion of the chick plumage there are still many follicles present which have not yet produced definitive feathers; these continue to erupt in orderly fashion until the pterylae are fully clothed. Thus it is in the marginal areas of the feather tracts that juvenile feathers first make their appearance. Only after the feather tracts are completely developed does moulting and replacement of chick feathers take place.

The juvenile phase may, and usually does extend to more than one generation of feathers but the /

the variation in moulting rate and seriation of feather replacement in the different areas is such that the number of generations intervening between the chick and adult types is not the same for all regions nor within a single region.

This stage is not a stable one as regards feather form; both the successive generations from an individual follicle and the serial development of feathers within an area exhibiting gradual changes in colouration, structure and pattern which approach progressively nearer the adult type.

(a) Order of Appearance.

By six weeks of age juvenile feathers may be distinguished on the shoulder and wing bow; in the latter they appear as new rows of feathers arising in a disto-proximal direction anterior to those rows of chick feathers already present. When this extension has been completed moulting and /

and replacement of the chick feathers begins. In this region the replacement of feathers appears to be a random process although in most of the other parts of the body it follows the order of feathering described for the chick. On the shoulder new feathers with a marginal zone of rusty red pigment arise in an postero-anterior order, extending forward to encircle the chick plumage. On the anterior edge some new, almost black feathers occur. (It is at this time and in this region that the sexes may be separated by reference to plumage differences). This process completed, the moulting of chick feathers begins and follows the exact order in which they were laid down. The moult takes place very slowly and requires a considerable period of time for its completion with the result that a seriation of juvenile plumage types gradually approaching that of the adult is found. Due to individual variability /

variability in length of moult adult feathers may first appear at the anterior end of the shoulder in some cases and at the posterior in others. Invariably, first juvenile feathers are to be found around the periphery of the shoulder region long after those in the centre of the area have been replaced by adult feathers.

On the breast the tracts widen and the new feathers differ from the older ones only in their larger size and the greater amount of melanin deposited in them. The extension completed, a second generation of pure black feathers appears on the median line of the tract; it originates, as in the chick, from growth foci in the anterior and posterior breast regions, and extends as described previously for the earlier stage.

The neck hackle appears to moult much more /

more readily than other areas and a continued orderliness of feathering cannot be distinguished in this region. After the frontal part of the head has been covered new feathers are added in the middle and lower part of the neck. Moulting of the chick feathers was frequent but there was obviously also an increase in the number of new feathers growing in. The area extended posteriorly to give rise to the "transitional" and cape feathers.

The last area to show juvenile plumage is the back. The narrow median band of chick plumage is extended laterally by the addition of juvenile feathers. Following this, moulting appears to occur somewhat at random but in later generations the original order established in the chick feathering is again evident.

No special juvenile form of feather was found on the thigh. The generation following the /

the chick plumage was of the adult type and repeated the order of chick feathering.

It was established that in no case did the moulting of the rectrices and remiges deviate from the general order shown in the chick. The second generation of feathers in these areas was mainly adult in form. The onset of the moult of the wing primaries varied in individuals but usually was found to take place in the 7th to 8th week from hatching. The process is very slow and is not completed until the bird has reached maturity, i.e. about an age of 6 months. The main tail feathers also moult directly to the adult form; beginning their replacement at about 5 weeks of age and completing the process some two months later. Sometimes a second moult was found to set in immediately after the completion of the first.

(b) Feather Types in Juvenile and Adult.

Wing Bow: /

Wing Bow:

1st. Generation (6 weeks) (Plate 7, fig. 2). In contrast to the square tipped chick feather they have a rounded end and there is a reduction in the number of barbules in the peripheral zone giving a suggestion of fringing; they are brownish red in colour with black pencillings unevenly concentrated to form roughly transverse bars, and a light coloured rhachis.

2nd. Generation (9 weeks) (Plate 7, fig. 3). Considerable variation in size and shape is shown but in general the shape is similar to that of first generation feathers; the brownish red colour becomes more obvious and the melanin is concentrated basally leaving only irregular splashes of this pigment in the apical third of the feather. The feathers have a fringed appearance distally, but except on the extreme /

extreme points of the barbs only the hooklets are missing. Later in this generation feathers with the vane solid black both apically and basally appear, the intermediate region being red with a few black stipples.

<u>3rd. Generation</u>. (13 weeks) (Plate 7, fig. 4). This stage is marked by the great increase of the red area in the feathers at the expense of the black, which is now restricted to the fluffy basal region, to a few small splashes on the red field and an occasional well defined apical spot. The depth of peripheral fringing is more marked than in the previous generation, but not yet devoid of barbules.

<u>Adult Type</u>. (16 weeks) (Plate 7, fig. 5). The adult feathers are broad with a rounded outer margin. A deep apical fringe, consequent on a lack of barbules, surrounds the solid /

solid part of the vane; the latter is shaped like an arrowhead with its apex pointing distally along the rhachis.

Shoulder:

Much the same sequence of changes occurs in the shoulder as in the wing bow feathers; indications of peripheral fringing, becoming gradually more evident through three successive feather generations give place to a well marked and extensive barbuleless area in the adult form. In the first juvenile phase (5 weeks of age), (Plate 7, fig. 7) the melanin is more evenly distributed and covers most of the vane apart from the lateral edges and rhachis. In succeeding generations (at 8 and 12 weeks of age), (Plate 7, figs. 8 & 9) it gives the impression of having receded towards the centre and base of the feather until in the adult form, first distinguishable /

distinguishable at 14 weeks, (Plate 7, fig. 10) it covers an area only slightly more extensive than it does in the wing bow. In this region changes in size and in the proportion of solid vane to fluff are noticeable: first juvenile feathers are about two-fifths longer than their chick predecessors and consist of three parts solid vane to two parts fluff; in later stages the fluff extends to half the total feather length. Adult shoulder feathers are much longer than those from the wing bow.

Breast:

The first anterior breast feathers (visible at 6-7 weeks of age) (Plate 8, fig. 12) are slaty black with a central strip of pale salmon colour which includes the rhachis. Some of this pigment is seen at the edges of the feathers. The barbs possess a complete complement of barbules.

The /

The larger feathers of the next generation (Plate 8, fig. 13) appearing at 10 weeks are slaty black apart from traces of the light coloured pigment at the apex.

By 12 weeks the pure black adult feathers (Plate 8, fig. 14) are in evidence; they show a slight indication of fringing at their distal ends.

On the posterior breast the chick feathering is replaced directly by the adult type, and the original semiplume - like feathers are succeeded by compact black feathers. (Plate 8, fig. 16). The change commences at about 6 weeks of age.

Neck Hackle:

The random replacement of hackle feathers (mentioned previously) and the gradation in colour changes makes the successive feather generations /

generations in this area difficult to determine. The first juvenile feathers are similar in size and shape to those of the chick but are more completely black centrally with cream coloured periphery. The next type distinguished are longer and broader, and have a fine yellowish strip along the rhachis: there is no definite fringing. (Plate 9, fig. 20). Succeeding feathers (Plate 9, fig. 21) become narrower and more pointed distally with well marked fringing; the barbuled area also delimits the black central core which is sharply pointed distally and widens gradually towards the base of the feather. The yellow central streak is fine and uniform.

Adult feathers follow this generation and in the centre of the area differ from it only in their much greater length.

At maturity this region shows a distinctive colour gradation in the feathers throughout /

throughout its length, from pure gold feathers on the head to others practically completely black at the base of the neck; the latter lack not only the yellow margin but their free fringe as well and are referred to as "transitional" feathers since they grade into the hackle on the one hand and the cape region on the other.

Back:

At 8 weeks ovally tipped feathers, much longer and with a more solid vane than the chick ones appear: they are slaty black with a cream, or mottled cream, apical portion which extends some distance down the rhachis (Plate 9, fig. 23). At twelve weeks brownish red feathers (Plate 9, fig. 24), mottled with black, and black basally are in evidence. The third generation (14 weeks) (Plate 9, fig. 25) shows a further restriction of melanin and the inception of fringing; further transitional forms appear before the adult type is /

is exhibited at 18 weeks, (Plate 9, fig. 26). Apart from its greater length and more pointed shape the latter is similar in every respect to the adult wing bow feather.

Saddle:

The first two generations of juvenile feathers (8 & 10 weeks) are similar to those of the back though the second is considerably longer and narrower (Plate 10, Fig. 27). The third (14 weeks) still resembles it in colour pattern but the feathers are again longer and more pointed; there is a definite apical fringe but the barbules are not yet completely lacking (Plate 10, fig. 28). The adult feathers (18 weeks) are long and lanceolate with a slightly widened base; they are deeply fringed right down to the top of the fluff and are golden red with a small black portion above /

above the fluffy base (Plate 10, fig. 29). In this region a gradation of colour is noticeable: the proportion of black to red in the feathers decreases in a medio-lateral direction.

<u>Cape</u>:

Not until the juvenile stage is reached are the cape feathers distinguishable from the adjoining neck hackle. At five weeks the first generation are slaty black with a cream mottled central stripe including the rhachis and traces of the same colour are found on the lateral edges (Plate 10, fig. 30). The second generation (10 weeks) are a more solid black with drab margins, and the light colour on the rhachis restricted to a fine distal line; a slight restriction of barbules causes the first indication of fringing (Plate 10, fig. 31). The third generation (16 weeks) are pure black with a red apex /

apex and a more conspicuous fringe (Plate 10, fig. 32). In the adult (18 weeks) the red apical portion becomes greatly increased at the expense of the black, and the fringing deepens: the feathers now resemble those of the back with the exception that the black area extends some way up the vane parallel to the limit of the barbules forming a second arrowhead. (Plate 10, fig. 33).

Thigh:

Chick feathers here are replaced directly by the adult type which is one third solid vane and two thirds fluff; they are black in colour, (Plate 8, fig. 18).

C. Summary of observations on juvenile plumage.

The juvenile phase in the plumage, arbitrarily defined to include all feather types between the chick plumage and the adult form, comprises a varying number of feather generations due /

due to variations in moulting rate and the seriation of feather replacement. The generations do not form discrete types but represent intermediate points in the continuous gradually changing character of the feathers between first juvenile and adult plumage.

The feathers are characterised by black and red pigmentation, and by the gradual appearance of fringing in successive generations in certain regions. The proportion of melanin is extremely high in the first juvenile feathers and becomes progressively less as maturity is approached except in the breast and thigh.

Variations in the degree to which these changes occur in different regions of the body, together with size differences result in the appearance of distinctive feather types characteristic of the various areas. This phenomenon also becomes more pronounced with age.

## Discussion.

## DISCUSSION.

Two main points emerge from this study of the feather sequence in the Brown Leghorn male from hatching to maturity: the first definitive chick plumage is a type apart, differentiated clearly from the later feathering by a colour pattern which never reoccurs in the male. On the other hand the juvenile plumage is not a discrete type but may be regarded as a modified version of the adult form; the first juvenile differs widely from the latter but the gap between the two types is bridged by a gradual change in the feather characters which results in the resemblance becoming progressively closer as the birds approach maturity.

The observance of the continuity of the process was made possible by the orderly manner in which the feathers are moulted and replaced which provided a continuous sequence of growing feathers, /

feathers, both on the different areas and within these areas; while a feather of one generation differed considerably from the next occupant of the same follicle, the intermediate grades were visible in other feathers of the pteryla which emerged seriatim along the rows of follicles, and appeared, in point of time, between the two generations. Such a phenomenon might be attributed to two possible causes: either (1) some stimulus influencing feather structure is undergoing a process of change (intensifying or weakening) throughout the growing life of the individual, or (2) there is a progressive alteration in feather response to a constant stimulus. That the first postulation appears more likely may be deduced from the description of the order of appearance of shoulder feathers where it was stated that "due to individual variability /

variability in the length of moult adult feathers may first appear at the anterior end of the shoulder in some cases, and at the posterior end in others". While this does not preclude the second hypothesis it seems reasonable to expect that a change in the inherent character of the feather would have been more consistently associated with the feathering order.

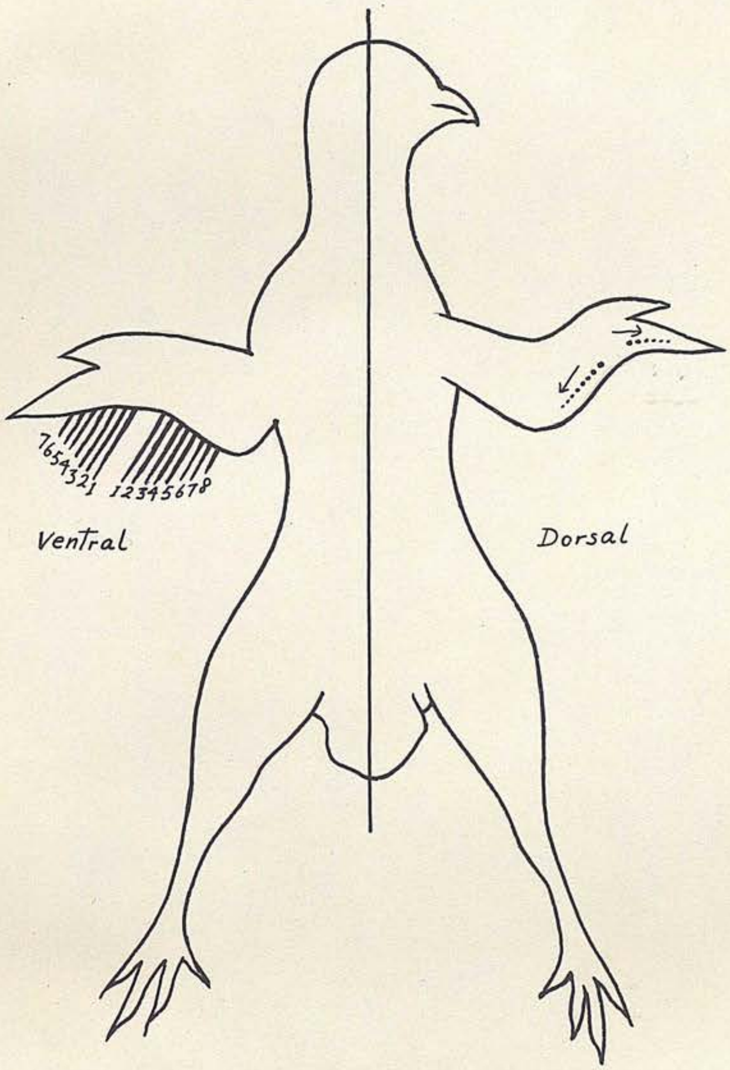
That certain stimuli, particularly the ovarian and thyroid hormones, have the ability to induce a change in feather type is evident from the publications referred to in the introduction, as well as many earlier researches, and from these it seems logical to consider the thyroid as a possible factor controlling the exhibition of the juvenile plumage phases. In the following sections attempts have been made to examine this possibility experimentally, and to decide whether the chick plumage /

plumage, though so distinctive in type, is not merely an extreme form of the graded series formed by the feathers of older birds. A histological study of the thyroid glands has also been undertaken to discover whether age changes in its structure, capable of correlation with the plumage phenomena, can be identified.

# Plate I

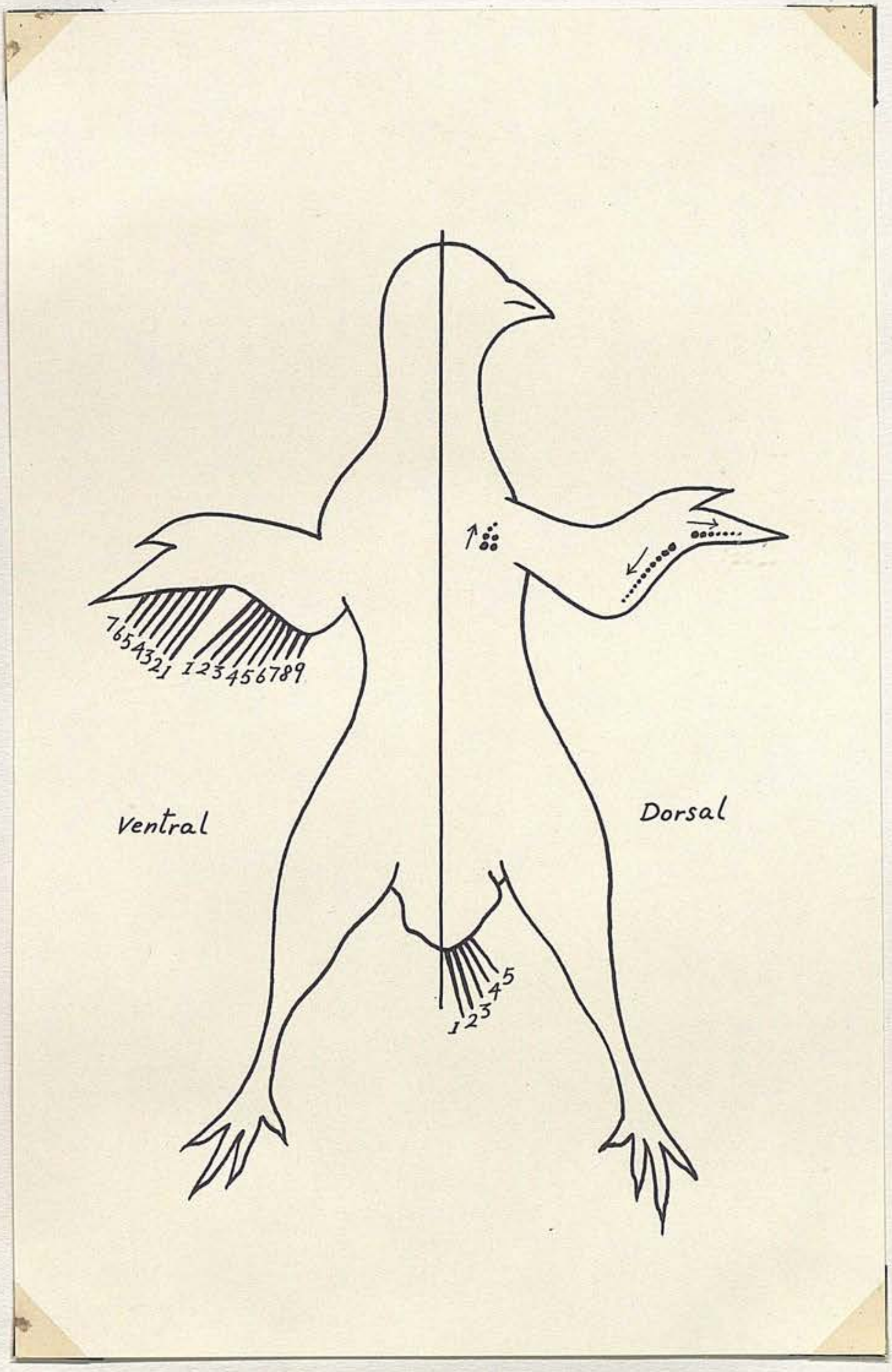
Down plumage of the baby chick

# Plate II



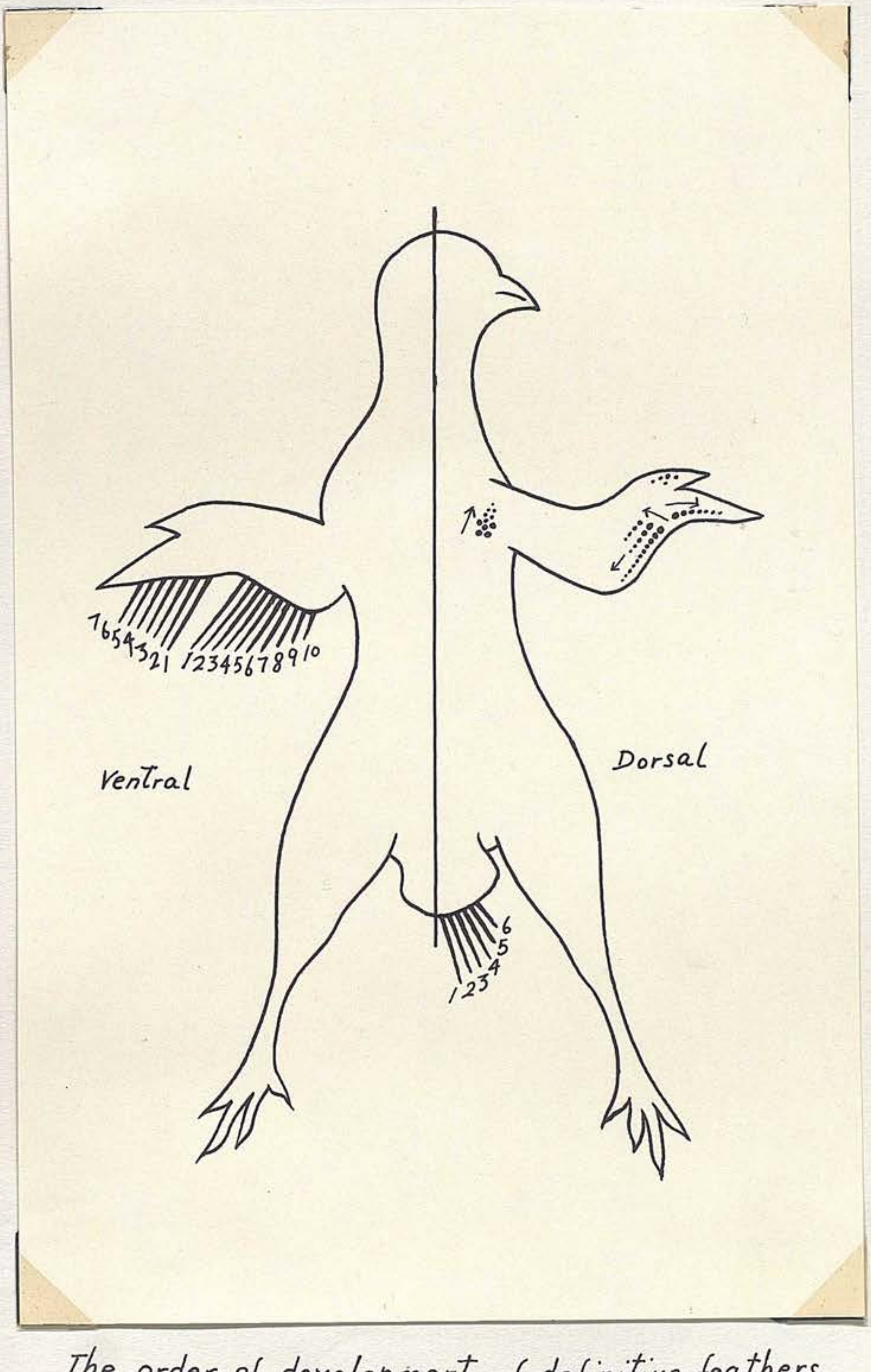

The order of development of definitive feathers in one day old chick.

# Plate III



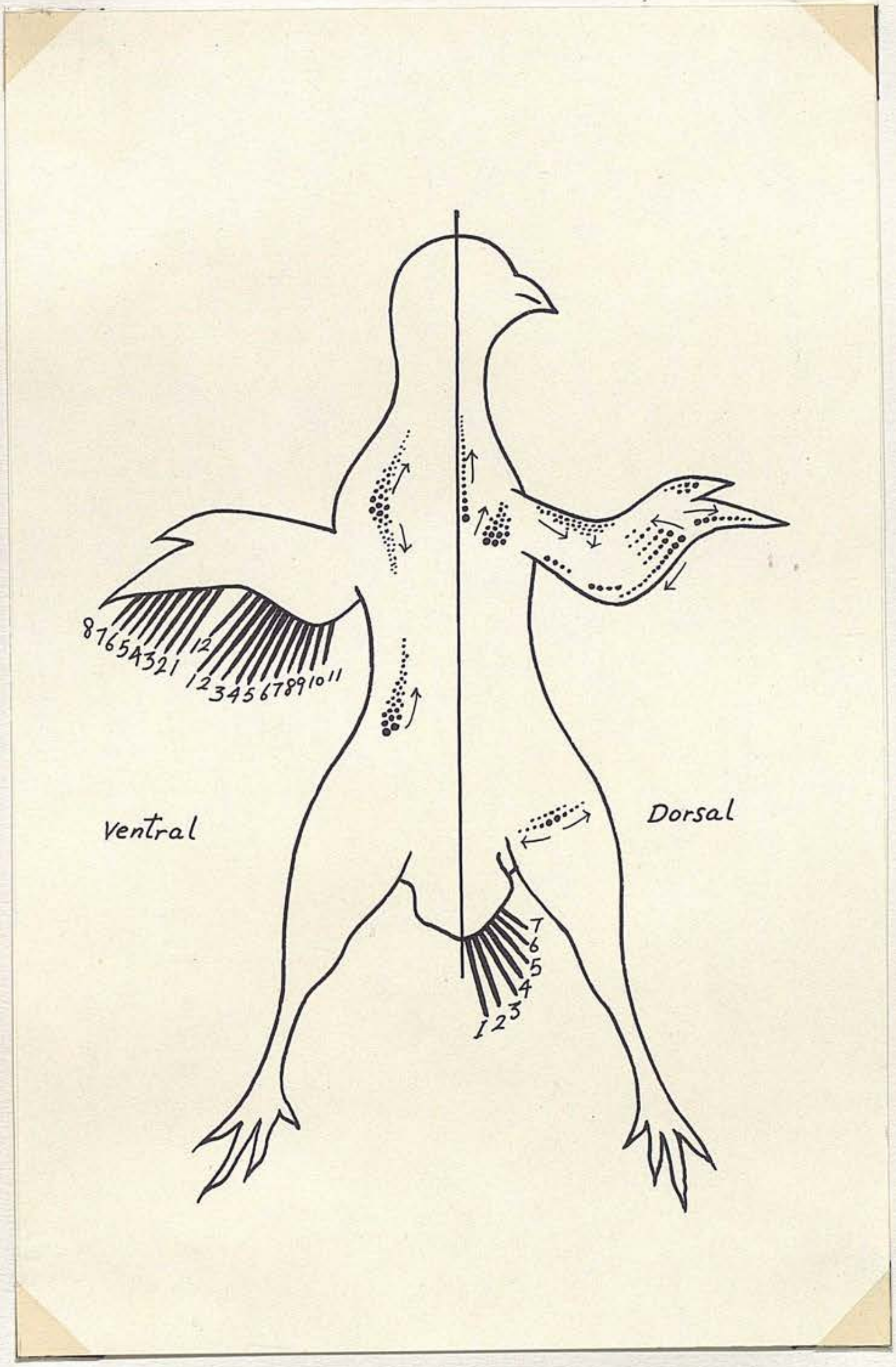

The order of development of definitive feathers in 3-day old chick.

# Plate IV



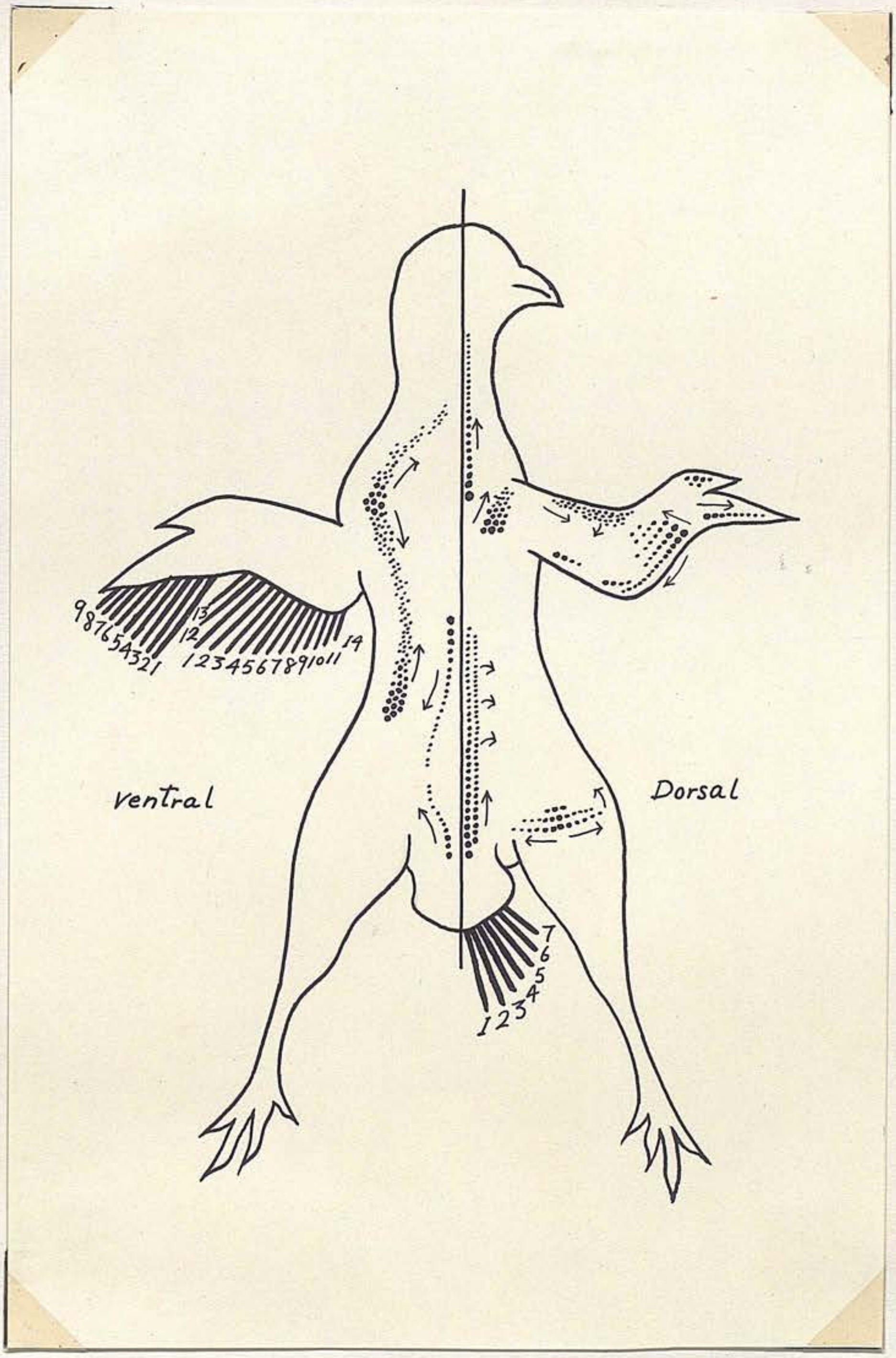

The order of development of definitive feathers in 8-day old chick.

# Plate V




*The order of development of definitive feathers in 15-day old chick.*

# Plate VI




The order of development of definitive feathers in 21-day old chick.

## Description of Plates

### Plate VII.

Figures I--5 represent the successive feather types appearing on the wing bow from hatching to maturity.

Fig. I. Chick feather.

Fig. 2. Juvenile feather of first generation.

Fig. 3. Juvenile feather of second generation.

Fig. 4. Juvenile feather of third generation.

Fig. 5. Adult feather.

Figures 6--IO represent the successive feather types appearing on the shoulder from hatching to maturity.

Fig. 6. Chick feather.

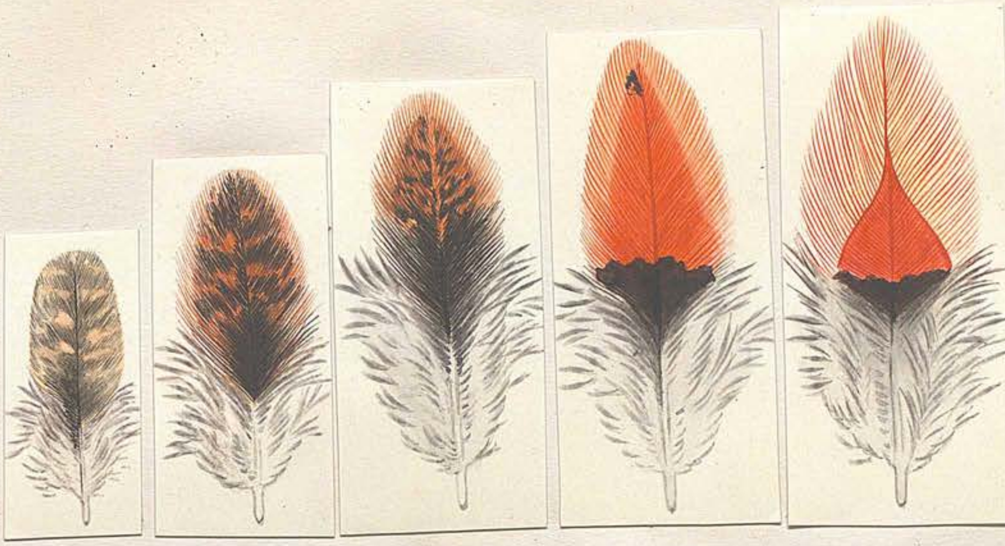
Fig. 7. Juvenile feather of fir st generation.

Fig. 8. Juvenile feather of second generation.

Fig. 9. Juvenile feather of third generation.

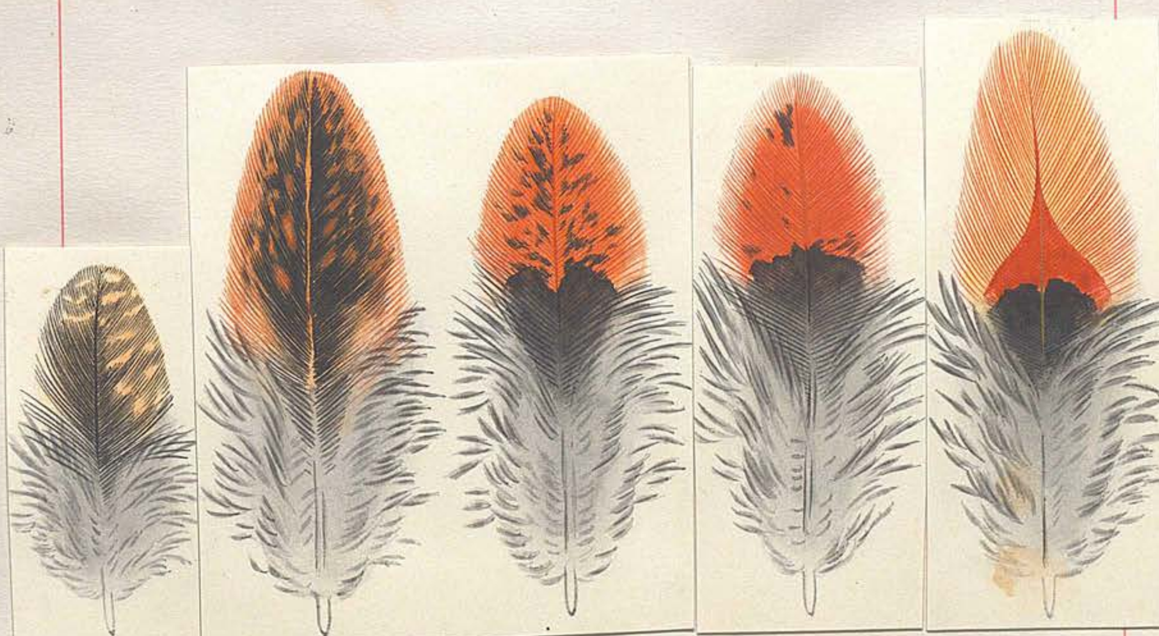
Fig. IO. Adult feather.

# Plate VII



1 2 3 4 5

Wing bow



6 7 8 9 10

Shoulder

Plate VIII.

Figures II--I4 represent the sequence of feather types appearing on the anterior breast from hatching to maturity.

Fig. II. Chick feather.

Fig. I2. Juvenile feather of first generation.

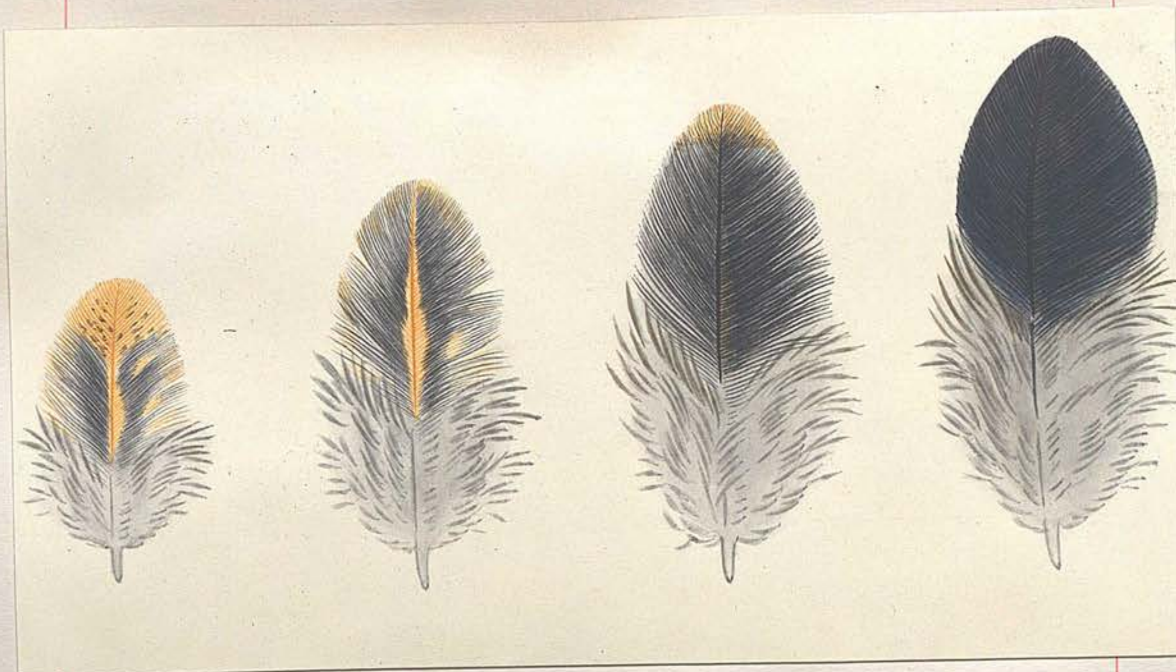
Fig. I3. Juvenile feather of second generation.

Fig. I4. Adult feather.

Figures I5 and I6 represent the chick and adult feather respectively of the posterior breast.

Figures I7 and I8 are of two successive generations of feathers (chick and adult) on the thigh.

# Plate VIII



11 12 13 14

Anterior breast

15 16 17 18

Posterior breast Thigh

Plate IX.

Fig. I9. Neck hackle at chick stage.

Fig. 20. Juvenile neck hackle of second generation.

Fig. 2I. Juvenile neck hackle of third generation.

Figures 22--26 are the successive feather types displayed on the back from hatching to maturity.

Fig. 22. Chick feather.

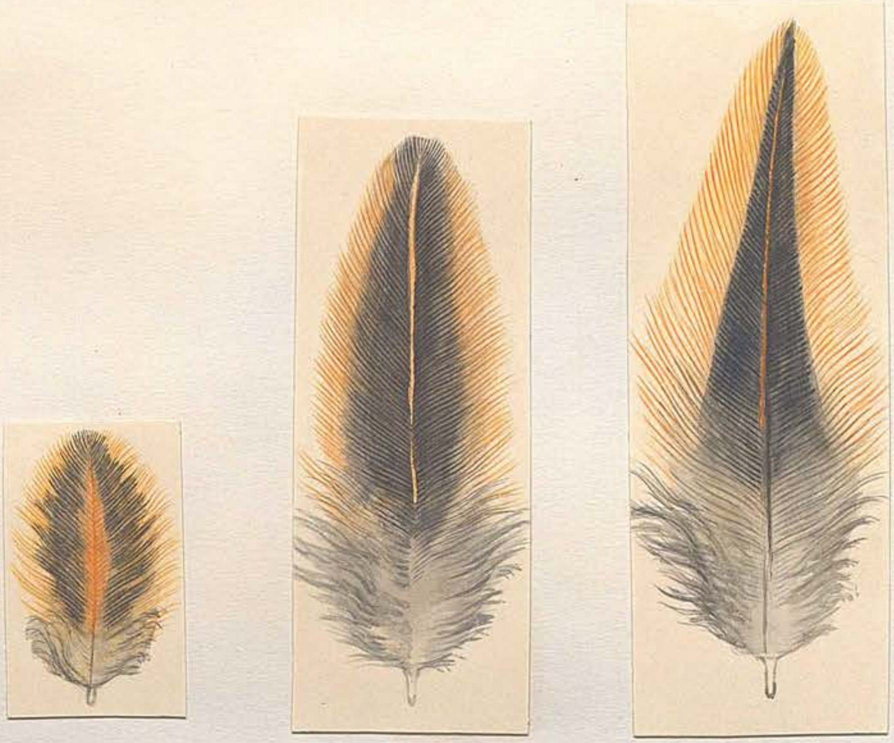
Fig. 23. Juvenile feather of first generation.

Fig. 24. Juvenile feather of second generation.

Fig. 25. Juvenile feather of third generation.

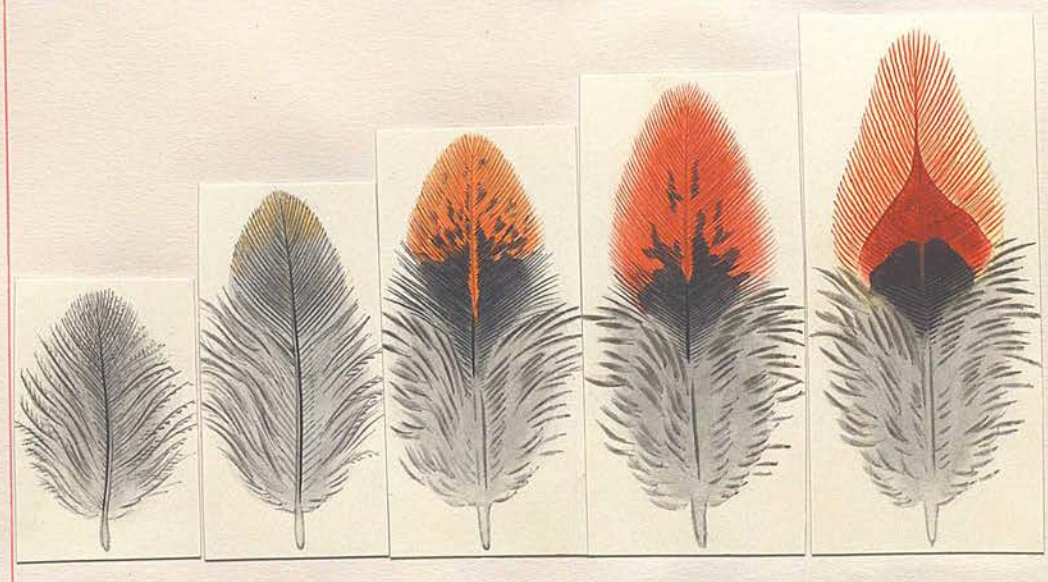
Fig. 26. Adult feather.

# Plate IX



19 20 21

Neck hackle



22 23 24 25 26

Back

Plate X.

Fig. 27. Juvenile feather of second generation on the saddle.

Fig. 28. Juvenile feather of third generation on the saddle.

Fig. 29. Adult saddle feather.

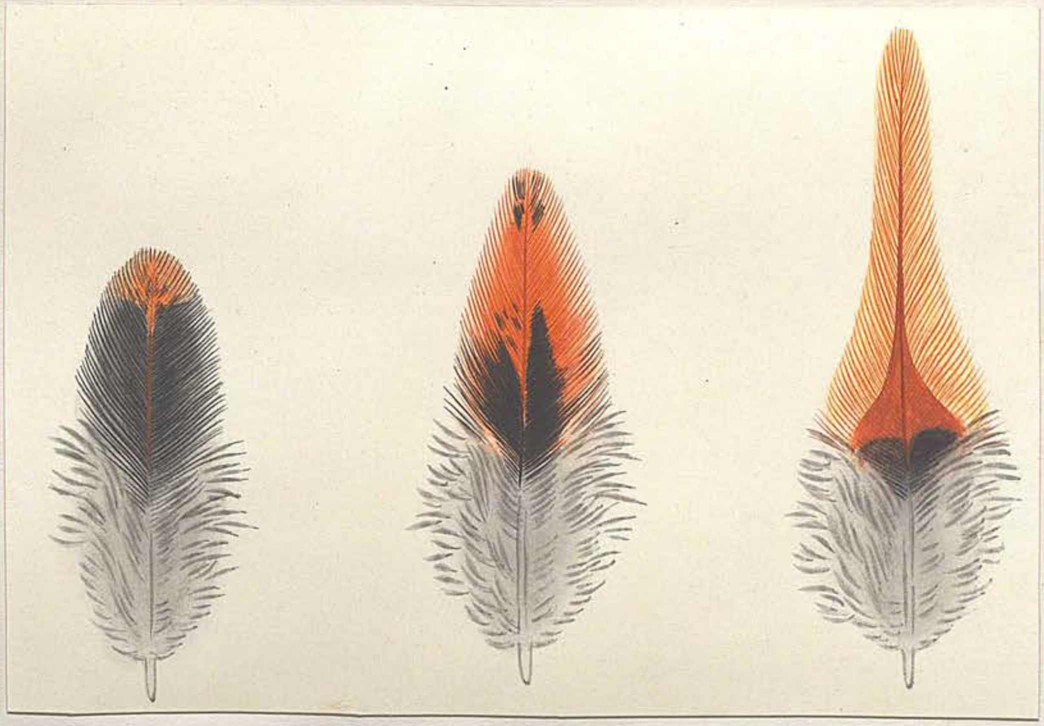
Fig. 30. Juvenile feather of first generation on the cape.

Fig. 3I. Juvenile feather of second generation on the cape.

Fig. 32. Juvenile feather of third generation on the cape.

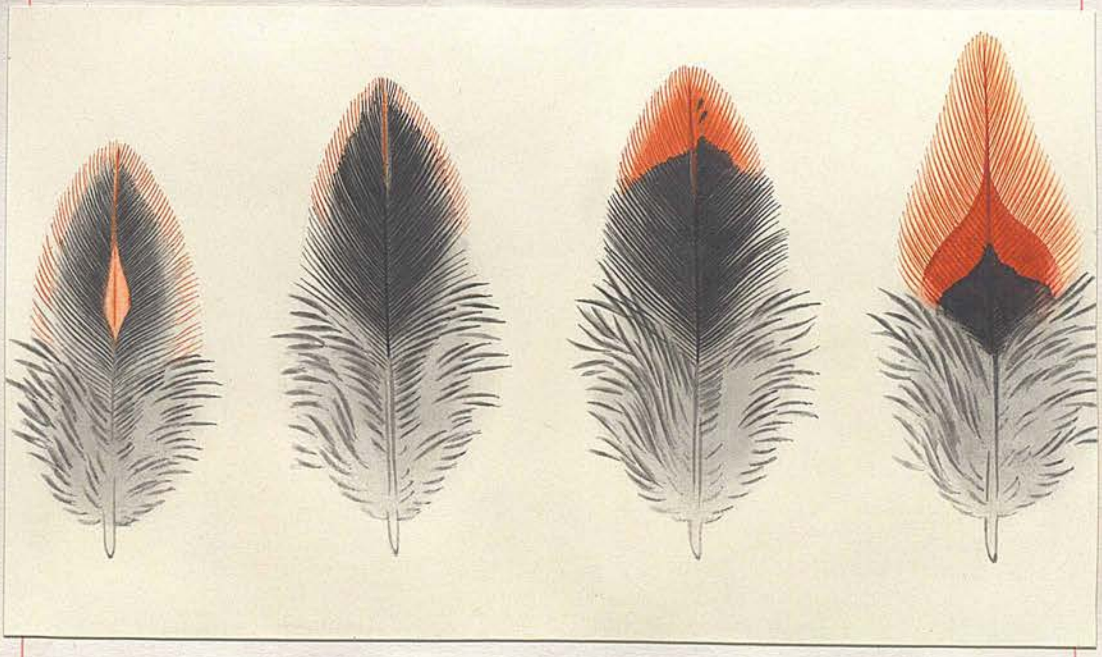
Fig. 33. Adult cape feather.

# Plate X



27 28 29

Saddle



30 31 32 33

Cape

## 11. The Developmental Morphology of the Thyroid Gland in Relation to the Appearance of Specific Plumage Types.

### Introduction.

Since Torrey and Horning ('22) found that female feathering may be induced in a male bird by means of thyroid medication many researches have been undertaken in the succeeding years the results of which have led to the general conclusion that administration of thyroid substance to the domestic fowl causes an excessive deposition of melanin pigment in the feathers and an increase in the number of barbules in those feathers which normally lack them to a greater or less extent. The changes induced in the male were similar to those normally found in the feathering of females. (Cole & Reid, '24, Torrey & Horning, '25, Horning & Torrey, '27, Martin, '29)

That /

That Crew & Huxley, ('23) failed to observe these changes led to a postulation based on their material, of a decreasing sensitivity of the feathers with increasing age of the bird. The use of massive doses of thyroid substance leads to the inhibition of pigment formation and white feathers ensue (Zavadowsky, '25). The work of Greenwood & Blyth ('29) on the Brown Leghorn confirmed the findings previously obtained with regard to the intensity of barbule formation and melanin deposition in the feathers but they were not inclined to attribute the modifications induced to an expression of the typical female pattern of this breed. They suggested that the development of the true female pattern in the feather could only be produced by the interaction of two endocrine products (1) that provided by the thyroid, causing an excessive deposition of melanin and (2) that provided by the ovary which exerts /

exerts an antagonistic effect to the preceding one resulting in the restriction of the melanin to a characteristic stippling of black on a drab background.

Thyroidectomy in the fowl has been found to decrease the number of barbules and to result in the depigmentation of the feathers, in so far as melanin is concerned, in the Brown Leghorn (Greenwood & Blyth, '29, Parkes & Selye, '37). In the completely athyroidic bird it is suggested that the feathers in all regions should be red and exhibit a complete absence of barbules.

Enough has been said of the relation of the thyroid gland to the development of adult plumage types in the Brown Leghorn to warrant an investigation of this gland with a view to determining its effect on the development of those intermediate plumage phases that appear successively /

successively from hatching until the adult plumage is assumed.

In the previous study an analysis has been made of the variation in succeeding feather generations grown during the juvenile phase. It has been noted that in certain regions as for example, the shoulder and cape, the feathers from the beginning of the juvenile phase indicate progressively a diminution in the amount of melanin and the gradual development of fringing of the feathers due to a decrease in barbule formation at the outer ends of the barbs. Based on the reaction of these feather characteristics in the adult bird to thyroid stimulation, it may be suggested that there is a progressive diminution in thyroid function through the stages of plumage characterising the juvenile phase. This assumption has led to study of this gland in the /

the growing chick.

Material:

Brown Leghorn chickens of varying age from the Institute stock were used. They were killed at biweekly intervals from the age of 4 weeks after hatching to maturity and at least four birds from each age group were examined. The glands were dissected out immediately after death and immersed in Bouin's fluid for $\frac{1}{4}$ of an hour. They were then removed and weighed, following which they were returned to the fixative and allowed to stand overnight. They were subsequently prepared for histological examination; sections $8\mu$ in thickness were cut, stained with Delafield's or Heidenhain's haematoxylin and counter stained with Eosin.

Results:

(a) The Variation in Thyroid Weight with Age.

Personal /

Table 1.

Relation of Body and Thyroid Weight to Age of Bird.

| No. of Birds. | Age in Weeks. | Body Weight in grams. | Thyroid Weight in grams. | Thyr. Wt. as % of Body Wt. |
|---|---|---|---|---|
| 10 | At hatch. | 45 | .0017 | .0038 |
| 5 | 4 | 131 | .0036 | .0027 |
| 5 | 6 | 248 | .0095 | .0038 |
| 14 | 8 | 297 | .0110 | .0037 |
| 10 | 10 | 642 | .0273 | .0043 |
| 12 | 12 | 784 | .0342 | .0044 |
| 8 | 14 | 865 | .0401 | .0046 |
| 6 | 16 | 1130 | .0649 | .0057 |
| 9 | 18 | 1248 | .0700 | .0056 |
| 5 | 20 | 1312 | .0704 | .0054 |
| 9 | 22 | 1867 | .1130 | .0060 |
| 12 | 24 | 2025 | .1210 | .0060 |
| 12 | 26 | 2108 | .1320 | .0062 |

Personal data relative to this study were considered inadequate and therefore they have been reinforced with material on this problem already available at the Institute. It will be seen from Table 1. that the increase in size of the thyroid gland with increasing age, after the first 8 weeks from hatching, is heterogonic relative to the increase in body size.

The thyroid weight of 6 months old birds shows an increase of about 88 times its weight in the newly hatched chick while the body weight in the same period has only increased about 46 times. When the amount of thyroid tissue present is calculated as a percentage of the total body weight it is found that this is lowest when the chick is four weeks old. From the age of 8 weeks the percentage increases until the 22nd week, after which no increase in the thyroid body weight ratio was obtained. The increase in size of /

of the thyroid gland can be attributed to two physiological processes (1) the growth and differentiation of the secretory tissue and (2) the deposition of the secretory substance as colloid in the vesicles as suggested by Latimer ('25). The data that have been obtained in this breed relative to the growth of the thyroid glands is similar to that obtained by Latimer ('25) in the Single Comb White Leghorn breed. Following the histological description of the thyroid from chicks of varying age an attempt will be made to discuss changes in the gland in relation to the successive types of plumage developed.

(b) The Histology of the Thyroid Gland:

Histological investigations on the mammalian thyroid, in both pre- and post-natal state have been undertaken by many authors (Chalmers Watson, '09, Jackson, '16, McCarrison, '17 /

'17, Cooper, '25) but similar studies on birds are not available to any extent although a brief account of the morphogenesis of the gland in this class of animals has been given recently by Eulin ('36).

In the fowl the thyroid gland consists of two discrete lobes situated on either side of the posterior end of the neck. They are faintly pinkish in colour and oval in shape. Both glands are to be found at the junction of the common carotid and subclavian arteries and the right one is embedded deeply in the thoracic air sac. The vascular supply is rich.

Histological examination of the gland from the newly hatched chick shows that it is composed of small round vesicles and groups of interstitial cell masses. (Plate 1, fig. 1). A thin /

thin connective tissue capsule encloses the gland, but no trabeculae could be found running inwards from the capsule as described in mammals. The small vesicles are usually enclosed by a thin basement membrane formed from a single layer of connective tissue which is absent in the case of the irregular cell masses. Numerous small capillaries are found in the interstitial spaces and penetrate both cell masses and vesicles. Young vesicles, with or without colloid deposited in the lumen are abundant. The vestiges of the embryonic pharyngeal arches still persist as cyst-like bodies composed of several layers of elongated epithelial cells. Vesicles in the peripheral zone of the gland appear to be in a higher state of secretory activity than those centrally located since they are usually larger in size and lined with a single layer of cuboidal or /

or columnar epithelium. Colloid is present in the vesicular lumina and is highly vacuolated, particularly where it is in contact with the epithelial cell lining. The cytoplasm of the secretory cells has an alveolar structure at the proximal region and contains some coarse granules; distally the structure is reticular, and the inner edge of the cytoplasm appears to be serrated. The nuclei are large and contain several deeply staining chromatic granules and one prominent nucleolus. In the central portion of the gland the vesicles are not only smaller in size but also show less secretory activity. Those composed only of small round masses of epithelial cells with deeply stained nuclei and a narrow rim of cytoplasm may be considered as an early stage of differentiation into vesicles. The presence of syncytial cell masses in which the boundaries of the individual components were obscured /

obscured suggests a pre-differentiation stage. Through the peripheral movement of the nuclei the cell group becomes hollowed out leading to the formation of the primitive vesicle. The contents of the lumen in the early formation of a vesicle consist primarily of cytoplasmic debris derived from the inner zone of the epithelial cell lining. Then follows a period of further growth during which secretory activity of the epithelium is initiated as indicated by an increase in the granular cell inclusions. Actively secreting vesicles are sometimes found in this region but they are smaller than those of the peripheral portion of the gland.

The structure of the gland in the 3 weeks old chick differs little from that of the preceding stage (Plate 1, fig. 2) except that an increase in both the number and size of the vesicles /

vesicles is seen. The intervesicular cell masses are still numerous and in the process of differentiation. Regarding the structure of the vesicles, two distinct types are present, viz. with vacuolated or non-vacuolated colloid content. The former are more numerous. The secretory epithelium of the vacuolated vesicles appears to be in the more active condition in that the distal end of the cells is emptied of secretory droplets and as a result this portion of the cytoplasm fails to take up the stain. Coarse cytoplasmic granules are invariably found at the proximal end of the cells and occasionally vacuolation of this region of the cytoplasm is met with. The epithelial cells of the non-vacuolated vesicles are cuboidal and contain fine granules which may be distributed evenly throughout the cytoplasm or occur as fine threads /

threads either radiating in all directions or in a direction parallel with the proximo-distal axis of the cell.

Some changes are found in the gland of the 4 weeks old chick. The secretory vesicles have increased both in number and in size. (Plate 1, fig. 3). The arrangement of the vesicles is more compact than in previous stages and the interstitial cell masses are consequently reduced. The vesicular epithelium indicates that at this stage the gland is very actively secreting. A large number of the vesicles show vacuolation both of the colloid substance and the cytoplasm of the secretory epithelium. The epithelial cells in the majority of vesicles are columnar, and the cytoplasmic structure usually granular in the proximal and reticular in the distal end of the cells. The vesicles in the immediate vicinity of the large sinusoid blood /

blood vessels show a higher degree of activity and the contour of the epithelial cells is obscured owing to the distension of the cytoplasm.

At the age of 6 weeks the thyroid gland indicates a high level of activity and differs in no significant structural details from that of the preceding age except that columnar epithelium is characteristic of a larger number of vesicles (Plate 1, fig. 4). The colloid content is stained faintly pink but vacuolation does not frequently occur. There is no increase in the amount of stored colloid, but a highly active epithelium is present. At this stage the vesicles are closely packed and the interstitial elements reduced. The blood supply is extremely rich both around the vesicles and among the intervesicular cell masses when present.

By the time the chick is 8 weeks old the gland /

gland appears to be decreasing in activity when compared with the previous stage. All the vesicles are closely packed and as a result there is a decrease in the amount of the intervesicular elements. (Plate 1, fig. 5). Distension of the vesicles is seen due to the gradual accumulation of colloid substance. The vesicular epithelium is cuboidal, or low cuboidal with spherical or oval nuclei centrally located in the cells. In some vesicles the epithelium indicates a rather higher level of activity and in these the cells are nearly columnar. The cytoplasm of the cuboidal cells is invariably finely granular and gives no evidence to suggest a high physiological activity. In a few vesicles both cuboidal cells and transitional types from columnar are seen. The colloid material in all cases is homogeneous and stained evenly pink.

At both 10 and 12 weeks of age the average size /

size of the vesicles in the gland has markedly increased and the interstitial cell masses have been reduced to a mimimum. (Plate 1, fig. 6, Plate 2, fig. 7). The vesicular epithelium is generally cuboidal and a low cuboidal type is frequently met with.

It is of particular interest to note in view of the colloid accumulation and the appearance of the epithelial cells generally suggesting a loss of secretory activity, that mitotic activity is somewhat intense among the epithelial elements. It is possible to assume that the mitotic activity, in itself is not an indication of secretory activity but is related to the gradual increase in intravesicular pressure due to the progressive storage of colloid, which in turn results in a stimulus to cell division in order to maintain a continuous vesicular epithelial lining.

When /

When the chick is 14 weeks old the gland is found to consist of closely packed medium sized vesicles. The heavy accumulation of colloid together with low vesicular epithelium indicates the relative inactivity of the glands at this age. (Plate 2, fig. 8). Although the gland as a whole suggests a low secretory activity, the vesicles in the peripheral zone still indicate a higher level of activity than those of the central zone as shown by their larger size together with the coarsely granular nature of the cytoplasm of the epithelial elements which is serrated where it is in contact with the stored colloid. In this region the colloid, in contrast to that found in the /

the centrally situated vesicles, is vacuolated.

At 16 weeks characteristic changes begin to appear in the structure of some of the epithelial cells and this is more marked in the peripheral vesicles. There is a tendency to flattening of the epithelial elements although even within a single vesicle the component cells may vary from columnar to flat. (Plate 2, fig. 9). In the latter the cytoplasm is reduced to a minimum and they are obviously inactive. There is also an increase in the amount of stored colloid.

The general structure of the thyroid from the 19 weeks old chick is similar to that of the previous stage except that regressive changes /

changes in the epithelial elements are more marked. In spite of the flattening of relatively large numbers of these, many cuboidal cells can still be found suggesting a much reduced activity of the gland as a whole. A point of interest is that at this stage intervesicular cell masses were found to be relatively abundant although they had not been observed to occur to any extent since the age of 8 weeks. (Plate 2, fig. 10). Although the significance of their appearance at this stage is not understood it may be suggested that they are responsible for the neo-formation of vesicles destined to replace those older ones in which the regressive changes already referred to have advanced so far as to lead to their ultimate destruction.

When /

When the thyroid from the 23 weeks old chick was examined it was found to have a much greater amount of colloid stored than any of the stages so far dealt with. The vesicles were lined with flattened epithelium in which the nuclei appeared elongate or oval (Plate 3, fig. 11). They were not so intensely reactive to the haematoxylin stain as were those from earlier stages. The cytoplasm of the cells was also much reduced in amount. Intervesicular cell masses were numerous and occasionally suggested an early phase in vesicular differentiation. Vascular supply to the gland on the whole was rather poor but some large sinusoid vessels were found in the intervesicular spaces.

## DISCUSSION:

For the purpose of this study it is necessary to attempt to correlate the variations in the microscopical anatomy of the thyroid gland during /

during the post hatching period in the development of the chick with the sequence of plumage types exhibited during this time. This implies the ability to interpret morphological structures in terms of physiological activity. Even with the modern development of cytological technique this offers many difficulties.

Although there is general agreement that the structural differences in the vesicular epithelium such as have been described in this report may be taken as indicative of grades of physiological activity, the mechanisms involved in secretion and excretion of the active principle of the gland are still in doubt. A similar position exists with regard to the function of the colloid substance found in the lumina of the vésicles at all stages in development. Bensley, (1916), has claimed that the secretion, formed at the outer pole of the secretory /

secretory cells, is destined for direct transport into the vascular channels. An alternative hypothesis by this author suggests that following the condensation of the secretion in the form of droplets in the individual epithelial cells these are subsequently extruded into the vesicular lumen. On this hypothesis the intravesicular colloid is the active principle of the gland, its physical nature being attributable to a secondary change. That the appearance of vacuolation in the peripheral zone of colloid indicates, not the liquefaction of the substance in preparation for absorption, but newly extruded secretory droplets which have not yet undergone a change in physical state from liquid to colloid has been suggested by Winiwarter, (1935) who found that similar vacuoles are present in thyroid vesicles of the foetal guinea pig at a time /

time when no colloid could be identified in the lumen.

The absence of knowledge of a satisfactory mechanism whereby the colloid, if it is to be considered as the active substance, subsequently enters the circulatory system does not invalidate the hypothesis of an indirect mode of secretion and excretion as can be shown by reference to the seasonal variation in the weight of the thyroids in the adult bird. Riddle (1927) has noted in the pigeon that the winter thyroid is much heavier, (due presumably to the increased amount of colloid deposited in the vesicles), than the summer thyroid. Galpin (1938) reported in the fowl a similar seasonal variation in weight and produced evidence relating the small size of the gland in the summer months to active reproductive functioning. From the data available at the Institute /

Institute it can be shown that the seasonal variation in thyroid weight is independant of the age of the bird. These facts are sufficient to suggest that the accumulated colloid may be utilised by the organism and is not to be considered merely as the deposition of excess secretory product such as might follow the direct mode of secretion and excretion postulated by Bensley.

It may be suggested that the heterogonic growth of the thyroid in relation to increase in weight of the organism as a whole during the post-hatching period follows from the increasing amount of colloid deposited in the vesicles of the gland. Associated with the increasing amounts of stored colloid structural changes in the secretory epitheluim such as have been described indicate a gradual decrease in secretory function from /

from about the 8th week. The onset of these phenomena agree reasonably closely in point of time with the development of the second juvenile feather generation, a phase characterised by the initiation of fringing and an increase in the amount of red pigment in the feathers, With increasing age changes in the morphology of the thyroid indicating a progressive increase in the amount of stored colloid together with further extensive modifications of epithelial cell types from columnar to cuboidal or flat have been found to occur. Associated with this the feathers show progressively more intensely those features which have been shown experimentally to be associated with a hypothyroid condition.

The cause of the changes in thyroid functioning with increasing age is not to be looked for in the relation between the morphology /

morphology of the gland and the assumption of specific feather types since the latter reflect only the level of the gland secretion in the circulation at the time of feather growth and development. The accumulation of colloid and associated cell modifications may be taken to indicate a decreasing demand on the gland by the organism at different stages in morphogenesis the causal factors involved being outside the scope of this study.


SUMMARY.

(1) An attempt has been made to estimate functional activity in the thyroid of the male fowl from hatching to maturity from an analysis of weight and histological structure of the gland at different ages.

(2) The histological studies indicate that the thyroid of the chick from hatching to

6 /

6 weeks is highly active. Following this period a progressive increase in the amount of stored colloid together with regressive changes in the cell components of the secretory epithelium suggests both a decreased secretory as well as excretory activity on the part of the thyroid.

(3) From 8 weeks of age until maturity is attained thyroid size increases heterogonically when compared with body growth as a whole due probably to progressive colloid accumulation.

(4) Changes in feather structure and pigmentation similar to those which follow an experimentally induced hypothyroidism have been shown to be increasingly evident during the successive feather generations of the juvenile phase. The onset of reduced activity in the thyroid (8 weeks) corresponds in point of time with the appearance of red pigmentation and fringing /

fringing in the feathers (2nd. juvenile feather generation).

## Description of Plates

Plate 1 (Camera lucida drawings).

Fig. 1. Thyroid of the newly hatched chick, showing the cuboidal epithelial cells, vacuolation of the colloid, and intervesicular cell masses.

Fig. 2. Thyroid of 3 weeks old chick. The vesicles have increased in size. The epithelium is cuboidal and the colloid vacuolated.

Fig. 3. Thyroid of 4 weeks old chick. Columnar epithelium present with cytoplasm, vacuolated in the distal end and granular in the proximal end of the cells; intervesicular cell masses reduced.

Fig. 4. Thyroid of 6 weeks old chick.. The vesicles are lined by columnar epithelium with cytoplasm serrated at region in contact with the colloid.

Fig. 5. Thyroid of 8 weeks old chick, showing cuboidal and low cuboidal vesicular epithelium.

Fig. 6. Thyroid of 10 weeks old chick. The vesicles have increased in size following the accumulation of colloid. Low cuboidal epithelium present.

Magnification 340 X.

# Plate I

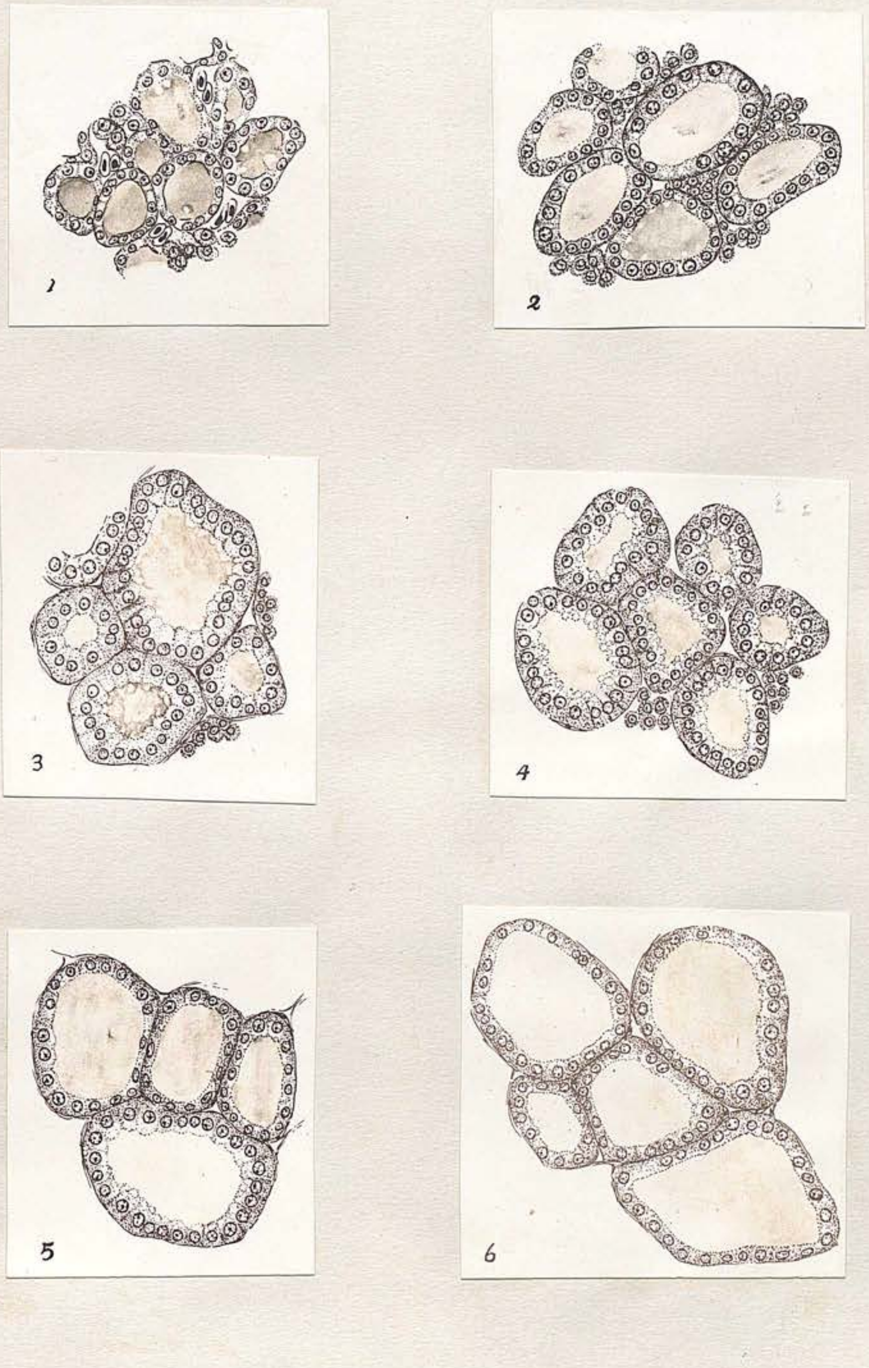


Plate 11. (Camera lucida drawings).

Fig. 7. Thyroid of 12 weeks old chick, showing the low cuboidal epithelium with finely granular cytoplasm.

Fig. 8. Thyroid of 14 weeks old chick. The structure differs little from the preceding stage.

Fig. 9. Thyroid of 16 weeks old chick, showing the tendency to flattening of the epithelial elements.

Fig. 10. Thyroid of 19 weeks old chick. The secretory epithelium is composed of both flattened and cuboidal elements. Intervesicular cell masses appear again.

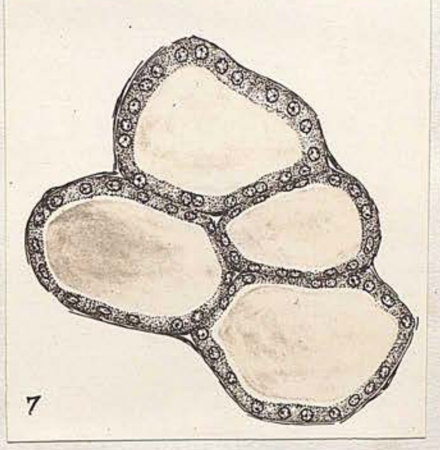
Magnification 340 X.

Plate 111 (Camera lucida drawing)

Fig. 11. Thyroid of 23 weeks old chick, showing the heavy accumulation of colloid.

Magnification 460 X.

# Plate II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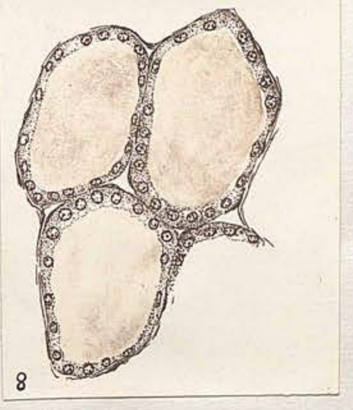
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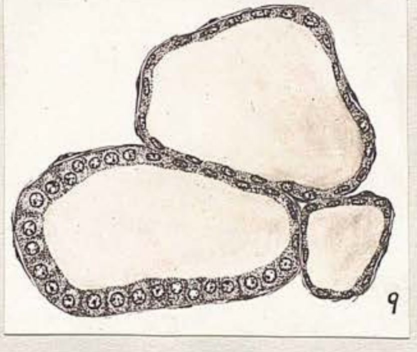
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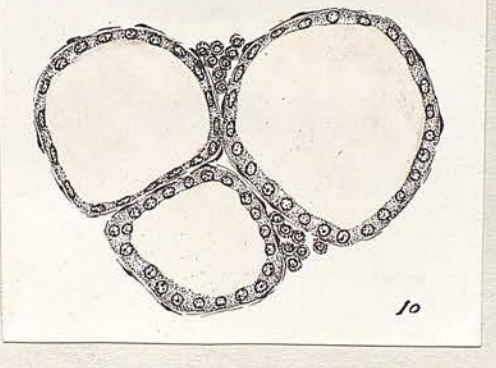
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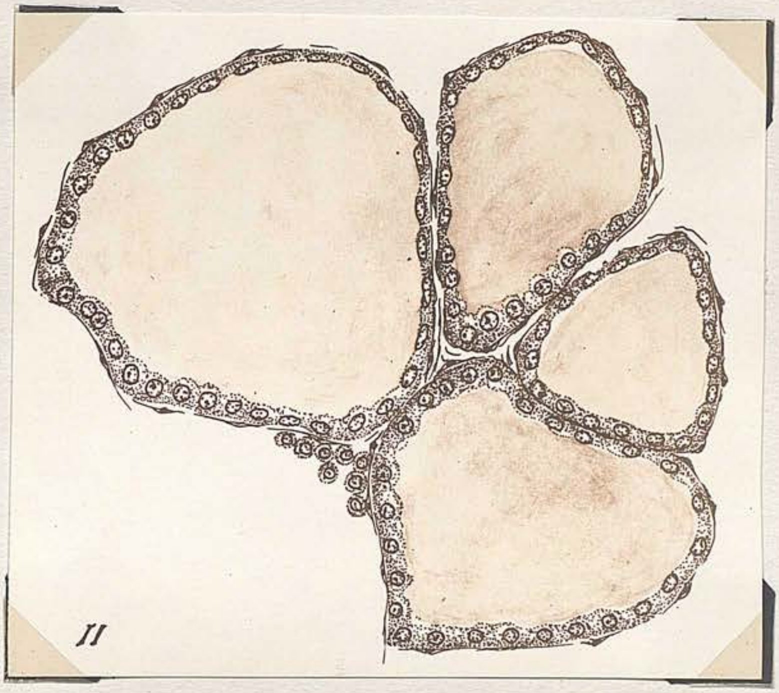
# Plate III



11

## III. The Effect of Hypo- and Hyperthyroidism on Plumage Characters in the Immature and Adult Male.

### Introduction.

In the preceding sections of this study a hypothesis has been evolved suggesting that the sequence of plumage types manifested by the Brown Leghorn male between hatching and maturity is the reflection of a gradually decreasing level of thyroid activity during this period. It was in order to examine this hypothesis further that the present investigation was undertaken. It concerns the comparison of the effect of thyroidectomy and thyroid feeding in males of different ages and the possibility that the experimental treatment might be instrumental in replacing the plumage characteristic of one age with that of an earlier or later generation.

## (A) THYROIDECTOMY.

### Material and Technique.

For this part of the experiment 50 newly hatched chicks, 20 six-week old cockerels, and 10 older males, varying in age from 6 months to three years, were operated upon.

The technique of the operation has been described by previous workers, (Greenwood & Blyth, 1929; Parkes & Selye, 1937) and only brief reference need be made to it here. The thyroid glands in the fowl are situated at the base of the neck, one on either side; the right is in rather a deeper position, embedded in the anterior thoracic air sac. The birds were deeply anaesthetised with Na-Evipan, and a median incision made ventral to the crop; to expose the right gland the oblique muscles to the crop had to be severed. Care is necessary to prevent haemorrhage as the gland lies in close contact with the jugular and near to the carotid /

carotid artery; injury to either is likely to prove fatal. No great difficulty was found in isolating the organ from the jugular by using a fine pair of forceps, but strict attention had to be paid to the severing of the thyroid artery as well as the thyroid vein. After extirpation, the connective tissue around the site was removed in an effort to prevent regeneration from minute residual fragments.

Results obtained in the course of these operations, and in a further series used in another study, suggest that cauterization should be avoided in thyroidectomy. It is generally recognised as a useful method of killing tissue remnants without haemorrhage, but while it is satisfactory from this point of view in thyroidectomy in the fowl, it usually leads to other harmful consequences. Most of the birds which were cauterised did not live more than one or two weeks after the operation; they

first /

first showed difficulty in respiration, then loss of appetite, and finally death ensued. The cause of death was not identified but it is possible that a branch of the nerve supply controlling respiratory movements was severed or severely damaged by cauterisation. On the other hand the same symptoms may be related to the destruction of the air sacs: damage to the right air sac is inevitable but not vitally important, but if both are destroyed respiratory disturbances with fatal results may occur.

The thyroidectomised birds were kept under the same conditions of husbandry as the thyroid-fed males, as were also groups of unoperated birds which served as controls for both series. Daily observations were made and any plumage changes recorded. The effect of thyroid removal was very conspicuous, and the completeness of the operation could be judged by observing the regenerating feathers, and by noting /

noting the behaviour of the comb which regresses in the absence of thyroid. Once indications of regeneration appeared, a second operation was usually undertaken.

## Results.

General Effects. Out of a total of 80 birds operated upon, only 17 of those successfully thyroidectomised survived long enough to allow of adequate observation of plumage behaviour; of these 6 were adults, 10 juvenile males and one, a baby chick. In the chick group removal of the thyroid glands appeared to be almost inevitably fatal as most of the chicks died within a month of the operation, and in the one final survivor removal was not complete. The ages at which the various birds were autopsied are given in Table 1. In each case a search was made post-mortem for residual thyroid fragments and any doubtful tissue was sectioned and examined microscopically.

Table 1.

Details of Thyroidectomised Birds.

| No. of Bird. | Age at Operation. | Date of Operation. | Post-operative Life. | Completeness of Operation. | Secondary Operation. (Days after the 1st.) |
|---|---|---|---|---|---|
| Baby Chick | | | | | |
| J. 2510 | 1 day | 23/7/37. | 102 days. | No. | - |
| Juvenile. | | | | | |
| J. 1820 | 6 weeks | 22/7/37. | 102 days. | No. | 66days. |
| J. 1819 | " | " | 96 " | Yes. | - |
| J. 1826 | " | " | 90 " | " | - |
| J. 1817 | " | " | 95 " | No. | 66 days. |
| J. 1802 | " | 24/7/37 | 94 " | Yes. | - |
| J. 1963 | " | 26/7/37 | Alive. | No. | 62 days. |
| J. 1931 | " | " | 102 days. | Yes | - |
| J. 1925 | " | " | 210 " | No. | 62 days. |
| J. 1961 | " | " | 114 " | Yes. | - |
| J. 2136 | " | 12/8/37 | 160 " | " | - |
| Adult. | | | | | |
| H. 5066 | 6 Months | 24/7/37 | 152 " | No. | 86 days. |
| H. 5027 | " | " | Alive. | Yes. | - |
| G. 988 | 2 years | 14/8/37 | 106 days. | " | - |
| F. 453 | 3 years | " | 59 days. | " | - |
| J. 1008 | 6 months | 15/10/37 | Alive. | " | - |
| J. 1260 | " | 22/10/37 | Alive. | " | - |

Retarded growth in the post operative period characterised the young operated birds: at five weeks the sole surviving baby chick weighed 63 grams as opposed to the flock average of 320 grams at this age. At 14 weeks, the time of its death, it weighed 230 grams. In the juvenile group too the skeletons were small compared with the controls but in a number the weight was almost up to normal; this was due to the heavy deposition of fat which had occurred both subcutaneuosly and in the abdominal region.

Plumage Changes

Chick. In the newly hatched chicks the feathering consisted of down with the tips of a few rectrices and wing flights showing. Following the operation contour feathers grew in very slowly and appeared normal in pattern. After about a fortnight, growth of feathers, as well as the organism as a whole, ceased in the 19 chicks under observation. That these effects were /

were not immediately apparent may be attributed to the continued presence of the hormone in the blood for a period after the thyroids had been removed: It has been shown that thyroxin is excreted very slowly (Harrington 1932).

The only survivor among the thyroidectomised chicks for a length of time sufficient to indicate plumage changes, was J 2510, and in this individual the extirpation was later found to be incomplete. Despite the occurrence of regeneration however the effect of hypothyroidism ultimately became visible in the plumage. Though the cessation of feather growth was not complete in this bird it was greatly retarded, and it was not until it was 2 months old that colour and structural changes in the feathers could be seen. At this time the barbules

barbules /

barbules at the periphery of the feather vane were found to be poorly developed, producing fringing, and the normal black and drab pencilling or barring disappeared because of the reduction in the amount of black pigment. The distribution of melanin was somewhat irregular and concentrated proximally: the basal colour became brownish red especially in the regions where the barbules were absent.. Such a type of plumage resembles the later juvenile pattern. Although these changes occurred not only in new feathers but also in the proximal parts of feathers already possessing a normal chick type tip, it has to be noted that they did not become visible until an age when the first dimorphic plumage would be appearing in the intact animal.

Juvenile and Adult. As will be shown later the rate of feather growth was also greatly retarded in these older birds, though it did not cease entirely /

entirely as in the chick. Apart from their smaller size the new feathers of the juvenile birds showed no real difference from those of the thyroidectomised adult. The plumage however differed markedly from that of the intact animal and lacked the characteristic regionalisation of feather types because colour and structural variations had become reduced to a mimimum.

In the accompanying series of illustrations, paintings of normal feathers, though not specifically referred to, are always included for comparison with those showing the effects of thyroid manipulation. They have been arranged so that in each group (a) represents a feather from a thyroidectomised bird, (b) a normal feather from the same region and (c) a feather from a thyroid fed individual.

In the feathers of the wing bow, shoulder, cape and back, (Plate 1. figs. 1a & 3a, Plate 2 figs. 5a & 7a) the predominant colour becomes a /

a uniform yellowish red: the normal brownish red is replaced by the lighter hue, and melanin is entirely absent except in the grey fluff region which is greatly reduced in size. The feathers become pointed and bristle-like (though actually less rigid than their normal homologues) due to the almost complete absence of barbules: only a few can be seen in a narrow region lying along either side of the shaft. Minor variations occur in the extent of these changes in the feathers of different body regions: for example, the reduction of barbules is greatest in the back feathers, and the proportion of fluff in the shoulders is not markedly reduced although in this region it is normally only poorly developed.

As might have been expected the saddle feathers show the most extreme effect being entirely deprived of melanin and barbules; the fluff is much reduced; (Plate 3, fig. 9a) the feather /

feather is more pointed and narrower than normal; in the thyroidectomised adult it is also much shorter. On the other hand the wing front feathers, (Plate 1, fig. 2a) which differ widely from the wing bow in the unoperated animal, take on an appearance very similar to the latter. The breast too, shows essentially the same changes, (Plate 1, fig. 4a) there is no difference in the resultant colour but the structural alterations are not so extreme: the fluff is much reduced but there is a narrow pointed solid portion of the vane lying along each side of the rachis.

On the neck the hackle feathers retain their usual contour but become wholly red and barbules are only developed along a fine strip adjoinig the **rhachis**: fluff is practically absent, (Plate 3, fig. 10a). The feathers of the transitional region between this and the cape are narrower and completely red. The remaining barbules form a narrow solid vane of elongated arrow-head /

arrow-head shape.(Plate 2, fig. 6a).

The operation appears to be without effect on the rectrices and wing primaries. In the secondaries the brown pigmentation in the narrow outer vane half is increased and the same colour appears on the rhachis which is normally black. In the degree of effect the wing bar feathers occupy an intermediate place between the contour and the long feathers, (Plate 2, fig. 8a). Here demelanisation and barbule deficiency again occur but are less extensive than in the former: the feather is deeply fringed but a large part of the vane still remains solid; the shape becomes more pointed and the fluff retains its normal proportion.

Summary of Thyroidectomy.

In the juvenile and adult birds thyroidectomy tends to reduce the contour feathers on all regions of the body to a uniform type of red barbule-less feathers with pointed tips.

The /

The obliteration of regionalisation is complete as regards colour but not entirely so as to structure: the degree of barbule deficiency varies with the regions: it is greatest in the saddle and least in the breast and transitional neck region.

In the chick the results were indefinite. Feather growth stopped after a fortnight in completely thyroidectomised individuals, and none survived for more than a month. In the incompletely thyroidectomised bird which survived feathers similar to those normally present in the later juvenile stages eventually appeared at 2 months - an age when ordinarily first juvenile feathering would have supervened.

## (B) THYROID FEEDING.

### Material & Technique.

For the first series of experiments on thyroid administration 6 newly hatched chicks, 5 six-week old cockerels, and 4 cocks aged from 6 months to two years were used. Control groups of 5 baby chicks, 6 juvenile and 5 adult birds were kept under observation at the same time. All the immature birds were from the same batches as those used for thyroidectomy.

Dessicated thyroid gland (B.D.H.) was the medium employed and the dosage given to the adult birds was 280 mg. per day; this quantity caused no obvious change in body weight and was therefore kept constant throughout the experiment. In the juvenile group where thyroid feeding began at six weeks the dosage was graded: 50 mg/day for the first week; 80 mg/day for the second; 120 mg/day for the next two weeks (9th & 10th); 160 mg/day for another three weeks, and 200 mg/day for a final four weeks(14th to 17th week). In relation to body weight this dosage was roughly proportional to that given to the adult birds.

The /

The amount administered to the baby chicks was relatively higher; and probably toxic as most of the group died within two months. This did not effect the experiment as the first definitive plumage had fully developed before the time of death. The dosages were as follows: first 2 weeks, 30 mg./day; 3rd and 4th , 60 mg./day; 5th and 6th, 90 mg./day; 7th to 9th week, 120 mg./day, and 10th to 12th week 150 mg./day. Details of the duration of treatment in the various cases are given in Table 2.

Table 2.

Details of Thyroid-Fed Birds.

| No. of Bird | Age at Beginning of Experiment | Medication Begun | Feeding Period (days) | Remarks |
|---|---|---|---|---|
| Baby Chick | | | | |
| J 2451 | 2 days | 17/7/37 | 115 | Died |
| J 2443 | " | " | 34 | " |
| J 2455 | " | " | 46 | " |
| J 2503 | " | 24/7/37 | 60 | " |
| J 2515 | " | " | 60 | " |
| J 2513 | " | " | 40 | " |
| Juvenile | | | | |
| J 1933 | 6 weeks | 27/7/37 | 30 | " |
| J 1929 | " | " | 24 | " |
| J 2142 | " | 11/8/37 | 60 | " |
| J 2156 | " | " | 61 | " |
| J 2144 | " | " | 98 | " |
| Adult | | | | |
| H 5077 | 6 months | 25/7/37 | 107 | Alive |
| H 5072 | " | " | 107 | " |
| H 2028 | 1 year | 14/8/37 | 120+ | " |
| G 849 | 2 years | " | 120+ | " |

## Results.

### General Effects.

There was no obvious effect on body growth; the birds appeared thin but this was not reflected by any significant difference in their weight in comparison with the controls. The adult cocks remained normally healthy but all the immature birds eventually died after varying periods of thyroid treatment. Whether this was due to too high a dosage of thyroid cannot be stated since there were no symptoms of hyperthyroidic disturbances prior to death.

In the juvenile and adult groups comb measurements were made every ten days for a period of three months from the initiation of the treatment, but there was no significant deviation from normal behaviour in this character.

### Effect on Plumage.

Chick. No difference in colour, pattern or structure /

structure resulting from the thyroid medication could be identified. Neither was there any appreciable alteration in shape or size.

Juvenile. In all the birds of this group it was found that feathers of the first generation were usually not affected. Succeeding generations, instead of gradually approaching the adult type, assumed the same colour pattern and structural characteristics of the first generation.

Adult. Here also the general reaction was to produce an increase in melanin and barbules but feathers in the different body regions showed this effect in varying degrees: those of the saddle and back being the least sensitive of the contour feathers. The pattern developed was not that of the female as suggested by Cole & Reid, (1924), but resembled most nearly the second generation of juvenile male feathers. The distinction between the male juvenile and female pattern /

pattern is obvious; in the former the melanin is distributed in massive pigment areas, whereas in the latter it forms fine pencillings. Contrary to the view of Zavadovsky (1925) the feathers of the thyroid fed birds were as a rule very stiff.

Barbules developed right to the margin of the feather vanes in all areas except the saddle, where they were still fringed distally, and the upper neck where a free yellowish border remained. No change in the proportion of fluff was noted in the cape, wing and shoulder feathers but in the back, saddle and neck hackle it appeared to have increased. Pointed feathers became more rounded, and this, in conjunction with the extension of barbules tends to give the feathers a structure similar to that typical in the female.

The extension of melanin to the distal parts /

parts of the vane was greatest in the cape feathers which were all black except a small red area apically, (Plate 2, fig. 5c). In the wing bow and shoulder the red areas were larger and tended to be situated peripherally, (Plate 1, figs. 1c & 3c). On the back the greater part of the outer half of the feather remained red with only some small black splashes. (Plate 2, fig. 7c). On the saddle the melanin, though in greater quantity than normal, is still less conspicuous than in the back region; it tends to be deposited mainly in the basal parts and along the rhachis to the extreme tip; where it extends to the margin the black area is barbuled. (Plate 3, fig. 9c). On the neck of the untreated bird the amount of black in the feathers decreases in a posterior to anterior direction, and in the increased melaninisation induced by thyroid feeding this gradation still persists, /

persists, the feathers of the lower neck being almost wholly black while those of the upper region have a black central cord with a yellowish free margin. (Plate 3, 10c). Breast feathers remain unchanged.

Summary of thyroid feeding.

1. No change resulted in the first definitive plumage of the chick.

2. In the juvenile phases the first generation of feathers was unaltered but subsequent generations continued to be of a similar type instead of showing a gradual approach to the adult pattern.

3. The plumage developed by the adult was also juvenile in type. The tendency was to produce black unfringed feathers but the extent to which this was realised with the dosage used differed in the different body areas, so that regionalisation was not completely obliterated.

(C). Induction of Juvenile Plumage in the Mature Cock and of Precocious Adult Plumage in the Growing Chick.

Although it has been shown that it is possible to produce a plumage type characteristic of the immature male in the adult by feeding thyroid gland, the results are somewhat incomplete in that only one juvenile stage has been induced, and the question arises whether the administration of different quantities of thyroid would result in the production of feather types of other generations. Furthermore the reverse effect, that is, whether it is possible to induce adult plumage precociously in the immature bird by thyroid manipulation has not been investigated. Experiments to test these two points will now be considered. In the case of the latter problem it was obviously necessary /

necessary to decrease the amount of thyroid hormone present below the quantity normally circulating in the young birds. As it was probable that compensatory hypertrophy of the residual tissue would make it impossible to achieve this by partial thyroidectomy, the birds employed in the test were first thyroidectomised and then fed with varying quantities of thyroid.

Material.

For the experiment with adult birds 6 two-year old cocks were used. Groups of feathers were plucked from areas on the wing bow, shoulder, cape, back and saddle. Four of the birds were fed a daily dose of 80, 160, 240, and 320 mg. of desiccated thyroid respectively, and this was continued until feather growth had been completed in the regenerated feathers. The other two /

two served as controls.

Four six-week old chicks were plucked in the same regions, and completely thyroidectomised. To ensure this a second exploratory operation was undertaken later in each bird. Three days after the removal of the glands thyroid feeding was commenced and daily doses of 10 mg., 15 mg., and 20 mg. were administered , two individuals receiving the intermediate dose; four control chicks of the same age were not plucked but their sequence of feather replacement was carefully noted.

Results.

1. In the Adult. Of the four cocks fed with various amounts of thyroid, that receiving the lowest dose (80 mg./day) showed no great effect on the plumage. The distribution of melanin was a little abnormal but still quite near to the adult pattern. The degree of feather change /

change in the two receiving the highest doses (320 mg. and 240 mg.) was marked but was much the same in the two birds, while the response in the bird receiving 160 mg. was intermediate between these and the first individual. The plumage resulting in the last three birds was peculiar in that although definitely juvenile in type the generation of juvenile plumage with which it corresponded was not the same in all areas. This becomes clear when the results are tabulated. (Tables 3a & 3b).

Table $3_a$.

Bird Receiving 240 mg. thyroid per day.

| Experimental Feather from Region of: | | Corresponding Normal Feather Type: | |
|---|---|---|---|
| Wing Bow | (Plate 4, Fig. 1) | 2nd. Juvenile | (Plate 4, Fig. 1′) |
| Shoulder | (Plate 4; Fig. 3) | 1st. Juvenile | (Plate 4, Fig. 3′) |
| Cape | (Plate 4, Fig. 5) | 2nd. Juvenile | (Plate 4, Fig. 5′) |
| Back | (Plate 5, Fig. 7) | 2nd Juvenile | (Plate 5, Fig. 7′) |
| Saddle | (Plate 5, Fig. 9) | 3rd Juv. but with deeper fringe. | (Plate 5, Fig 9′) |

Table 3b.

Bird receiving 160 mg. Thyroid per day.

| Experimental Feather from Region of: | | Corresponding Normal Feather Type: | |
|---|---|---|---|
| Wing Bow | (Plate 4, fig. 2.) | 3rd Juvenile | (Plate 4, fig. 2'.) |
| Shoulder | (Plate 4, fig. 4.) | 3rd Juvenile | (Plate 4, fig. 4'.) |
| Cape | (Plate 4, fig. 6.) | 3rd Juvenile | (Plate 4, fig. 6') |
| Back | (Plate 5, fig. 8.) | 3rd Juvenile | (Plate 5, fig. 8'.) |
| Saddle | | Slightly modified adult. | |

It will be seen that in the first bird the effect was more extreme in the shoulder than elsewhere, whereas in both the effect in the saddle lagged behind that in other regions. The saddle feathers of the second bird though obviously showing an increase in the amount of melanin and barbules were insufficiently altered to be comparable with juvenile feathers of this region.

2. <u>In the Juvenile.</u>

In the group of thyroidectomised chicks, only two receiving the intermediate dose of thyroid (15 mg. per day) developed plumage of the adult type. In one the effect was particularly good: the wing bow feathers (Pl. 6, fig. 11) were indistinguishable from those of the adult (Pl.6, fig. 11′) and the shoulder feathers (Plate 6, fig. 10) showed almost as close a resemblance to the mature type (Plate 6, fig.10′). On the back (Plate 6, fig. 12) /

fig. 12) the barbules were less well developed than in the adult (Pl. 6, fig. 12') and consequently the characteristic arrow-head shape of the solid part of the vane was not so clear. The saddle feathers (Pl. 6, fig. 13) again show the structure typical of the mature plumage (Pl. 6, fig. 13').

It was interesting that in both the birds which did not respond with mature feathering the dosage appeared to have been inadequate despite the fact that the one of them was receiving the greatest daily amount of thyroid. This suggests that considerable individual variation in response or powers of assimilation may occur.

(D). Growth Rate of Feathers in Normal, Thyroidectomised, and Thyroid-Fed Cocks.

It has been evident in the present study as well as in earlier researches that the amount /

amount of thyroid present influences the rate of feather growth, and in regard to the response of feathers on various body areas Lillie & Juhn (1932) suggested that hormone threshold was directly proportional to rate of growth. In view of this it appeared desirable to make a comparison of feather growth in the thyroidectomised and thyroid fed birds used in this study, and to examine the extent to which it differed from that of normal birds in the various body regions.

The structure of feathers and the variations they undergo under experimental conditions offer certain difficulties to the accurate determination of growth changes; for instance axial growth rates do not take into consideration variations in barb length. Since however the purpose of the present test is to compare /

compare growth in normal and experimental birds relative, not actual changes, are all that need be examined. These have been obtained by two sets of measurements, - (1) the time taken for completion of growth from the date at which the feather first pierces the skin, and (2) the number of barbs on the feather shaft. From these the average number of barbs laid down per day has been calculated. (Table 4).

Four thyroidectomised, four thyroid-fed, and two normal cocks provided the data. The thyroid-fed birds received a daily dose of 280 mg. dessicated thyroid. Six body regions, wing bow, shoulder, back, saddle, back and cape, were selected and patches of feathers removed from them on each bird. Care was taken to make the denuded areas as nearly as possible at the same point on each region.

Table 4. /

Table 4.

Comparison of Feather Growth in Experimental and Control Males.

| Region | Average No. of Barbs/Feather. | | | | | | | | | Av. Growth Period (days) | | | Barbs/day. | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | A | | | B | | | C | | | | | | | | |
| | L | R | T | L | R | T | L | R | T | A | B | C | A | B | C |
| Wing Bow | 118 | 120 | 238 | 198 | 194 | 392 | 192 | 191 | 383 | 79.5 | 53.5 | 40.0 | 3.0 | 7.3 | 9.5 |
| Shoulder | 208 | 208 | 416 | 267 | 261 | 528 | 276 | 276 | 552 | 72.5 | 53.5 | 41.7 | 5.7 | 9.8 | 13.2 |
| Back | 159 | 130 | 289 | 243 | 238 | 481 | 224 | 224 | 448 | 82.0 | 58.5 | 51.0 | 3.5 | 8.2 | 8.8 |
| Saddle | 188 | 190 | 378 | 327 | 317 | 644 | 337 | 336 | 673 | 90.5 | 74.5 | 59.0 | 4.2 | 8.6 | 11.4 |
| Breast | 196 | 196 | 392 | 239 | 229 | 468 | 235 | 237 | 472 | 78.0 | 56.5 | 44.2 | 5.0 | 8.3 | 10.7 |
| Cape | 182 | 182 | 364 | 256 | 257 | 513 | 244 | 249 | 493 | 83.0 | 59.0 | 47.0 | 4.4 | 8.7 | 10.5 |

A:- Thyroidectomised birds; B:- Normal; C:- Thyroid-fed.
L:- Left vane half of feather; R:- Right vane half; T:- Total.

It will be seen from Table 4 that the number of barbs on the feather was decreased markedly by the removal of the thyroids but that the administration of extra thyroid had no effect. On the other hand the period required for feather growth was shortened significantly in the thyroid fed birds, and similarly lengthened in the thyroidectomised group.

## DISCUSSION.

The results of the experiments on thyroidectomy and thyroid feeding described here are in sufficiently close agreement with the general findings of earlier authors (see introduction to section on thyroid histology and Greenwood & Blyth 1938), to make a detailed comparison with these unneccessary. Only the suggestion of Cole & Reid (1924), that thyroid feeding produces the female pattern in the plumage of the Brown Leghorn male, impinges contrarily /

contrarily on the hypothesis under consideration; it is at variance not only with the present observations, but also with those of previous workers (Horning & Torrey 1927 ; Greenwood & Blyth 1929) and it therefore seems justifiable to consider that their conclusion was erroneous.

As a whole the experiments have produced results which are still consistent with the hypothesis that juvenile plumage represents an expression of hyperthyroidism as compared with that displayed by the adult. It was to be expected on such grounds that thyroidectomy would reduce the plumage characteristic of the various ages to a basal type, and this is what occurred; in both juvenile and adult individuals melanin and barbules practically disappeared from the feathers leaving them red and heavily fringed. The slight indications of regional differences still recognisable in the minor variations in amount /

amount of solid feather vane may result from inherent differences in the feathers of the various body areas, or be the reflection of their differential reaction to minute residual thyroid fragments, though if these were present they were so small as to be undetected post mortem.

With regard to the first definitive plumage, viable athyroidic baby chicks were not obtained but in the one incompletely thyroidectomised member of this group that survived the tendency to a red barbule-less type of feathering was also apparent. The significance of this change is not clear however for the modified feathering did not appear until 2 months of age while the initiation of juvenile plumage usually occurs about 6 weeks. Even taking into consideration the slowness with which they developed, it cannot be /

be said with certainty which generation of feathers they replace, and further experimentation must be undertaken before it can be decided whether or not the type of the first definitive chick plumage can be influenced by thyroidectomy.

The data with regard to thyroid feeding provides more direct evidence of the relation between juvenile and adult plumages. In the mature cocks administration of thyroid led to the exhibition of feathering with definite juvenile characteristics, while with similar treatment birds of the second and third juvenile stages exhibited only feathers of the first juvenile type. Though the adults had the same amount of thyroid in relation to body weight as the younger birds, the degree of hyperthyroidism they showed was not so great, but this cannot be assumed to indicate a differential reaction to a proportionate dose for their own thyroid glands /

glands were still present and it is not known to what extent the latter were affected by the hormone administered. Our hypothesis infers that either the feathers of the immature birds are more responsive to thyroid, or that the thyroid gland is relatively more active prior to maturity. In the latter eventuality it is reasonable to suppose that the adult and immature glands would not be repressed by the treatment to the same extent, and it cannot therefore be suggested that the total concentration of hormone present is proportional.

The degree to which the bird's own thyroid is repressed may also provide an explanation of why the medication was without effect on the first juvenile plumage. On the other hand it may be that this plumage manifests the most extreme type of reaction obtainable, and that there is some limiting factor which prevents /

prevents the complete melanisation of the feathers; there was no indication that the hormone administration was capable of replacing first juvenile by chick plumage.

In the latter the treatment was also without effect, and this appears to be a parallel result with that obtained by earlier workers in the adult female where the plumage is similar to that of baby chicks of both sexes. It has been suggested (Greenwood & Blyth, 1929) that in the hen the melaninising influence of the thyroid gland on the plumage is restricted by the ovarian hormone, and that the same hormone, present in the yolk sac, performs a similar function in the baby chick. However the fact that it has been impossible to demonstrate clearly any effect of extirpation in the baby chicks makes it uncertain whether the thyroid glands are really involved in the production of the first definitive plumage. /

plumage.

Perhaps the most significant part of the experiments was the ability to demonstrate that it was possible, by thyroid manipulation, not only to replace adult plumage by juvenile in the mature male but also to obtain the reverse, the exhibition of adult plumage in the immature bird. In the cocks the amounts of thyroid substance used were only effective in producing plumages comparable with those of the 2nd and 3rd juvenile generation respectively. Whether it would be possible by heavier doses to induce the 1st generation type cannot be decided from the present material; the fact that the heaviest dose produced a similar effect to that of the second heaviest suggested the operation of a limiting factor, but on the other hand, the results of the administration of graded doses to the juvenile group /

group indicated that considerable individual variation in the response may occur.

A problem raised by the results in this section is that the degree of feather modification was not parallel in all regions of the body. This was particularly evident in the thyroid-fed adult males, where the effect was relatively less marked in the saddle, and was also indicated in the juvenile birds by the less perfect imitation of the adult back feather. Such irregularities might lead to the conclusion that changes in the activity of the thyroid gland are not alone sufficient to account for the sequence of feather types from juvenile to adult stages, and that some alterations in the relative response in the different body areas must also occur.

Greenwood & Blyth (1929) came to the conclusion that the feather types on the different /

different body regions of the cock represented varying degrees of response of a basal type to the activity of its thyroid glands, the feathers of the saddle, wing bow, cape, and breast showing increasing amounts of thyroid influence in that order. This is in line with the present observations on the results of thyroid manipulation and serves as an explanation of the variations which occurred in one and the same individual: thus it was to be expected that the effect of thyroidectomy on the contour feathers would be greatest in the saddle and least on the breast, and also that the response to thyroid feeding would be least marked in the saddle feathers.

The postulation of Lillie & Juhn (1932) that feather response is directly proportional to rate of feather growth led to the expectation that /

that the relative growth rates in the body areas would fall into the same sequence, but a comparison between regions, as measured by the barbs laid down per day does not fulfill this condition: the saddle and breast feathers, representing opposite extremes of effect, show an intermediate rate of growth, while the wing bow and shoulder feathers, very similar in type, show extremes of growth. Further there is no indication that these regional growth differences tend to become obliterated under conditions of thyroidectomy and thyroid feeding. The only suggestion of a repetition of the feather type sequence in the measurements taken was in the average barb numbers; the difference in feather length makes a direct comparison of this character in different regions impossible, but when the number of barbs on the feather following thyroidectomy was /

was expressed as a percentage of the normal number, the order of degree of reduction, from greatest to least was saddle, back, wing-bow, cape, shoulder and breast, the actual figures being, 0.59%, 0.60%, 0.61%, 0.71%, 0.79%, and 0.84% of the normal number. While such a finding can add nothing constructive to the discussion of the relation of feather growth rate to hormone response, it demonstrates the fact that the structural deficiencies which result from the removal of the thyroid glands are not restricted to the barbules, but involve also the barbs themselves, and that the degree of this deficiency falls in the same order as do the other feather changes. That thyroid feeding had no apparent effect on this character suggests that there is fairly low limit to the number of barbs which can be produced on a feather by /

by thyroid administration, and that this is reached prior to the saturation point of barbule formation. The figures indicate that the total number of barbs attainable is different in the different body regions, a condition which is to be expected from the varying feather lengths.

## Description of Plates

### Plate I.

Fig. Ia. Wing bow feather of thyroidectomised bird, showing the deprivation of melanin pigment and barbules, fluff much reduced.

Ib. Wing bow feather of the normal bird.

Ic. Wing bow feather of thyroid fed bird, showing the increase of melanin pigment and of barbules.

Fig. 2a. Wing front feather of thyroidectomised bird. It becomes purely red and deeply fringed.

2b. Normal wing front feather.

Fig. 3a. Shoulder feather of thyroidectomised bird.

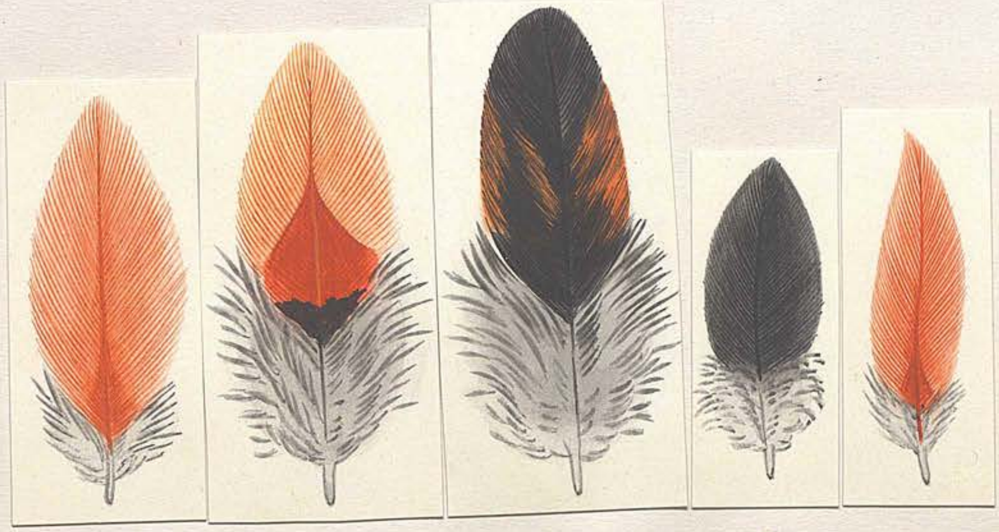
3b. Normal shoulder feather.

3c. Shoulder feather of thyroid fed bird.

Fig. 4a. Anterior breast feather of thyroidectomised bird.

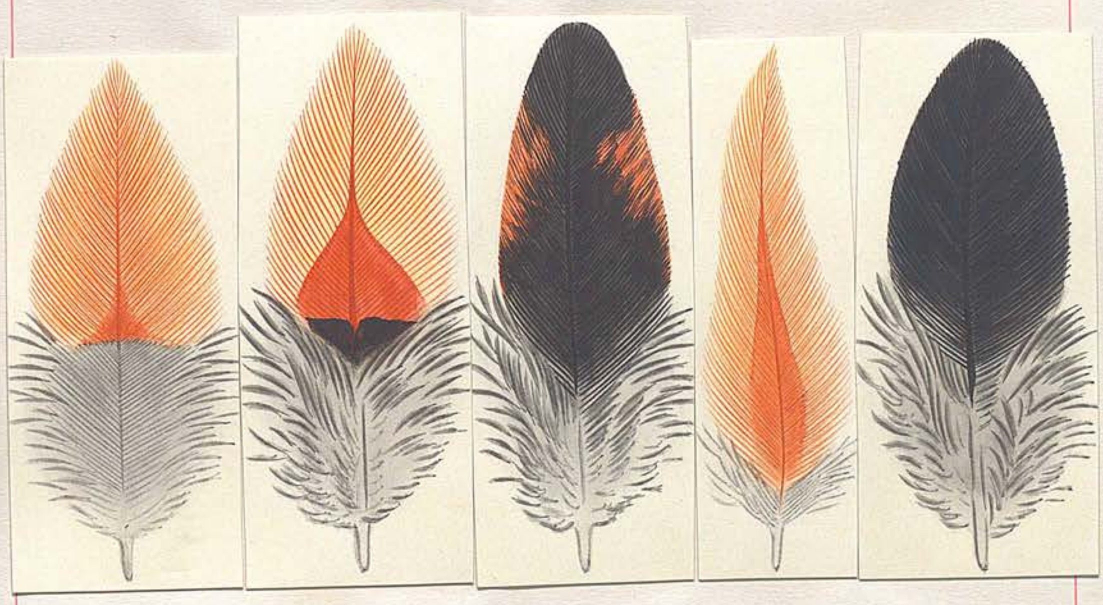
4b. Normal anterior breast feather.

# Plate I



1a 1b 1c 2b 2a

wing bow wing front



3a 3b 3c 4a 4b

Shoulder Anterior breast

Plate II.

Fig. 5a. Cape feather of thyroidectomised bird.

5b. Normal cape feather.

5c. Cape feather of thyroid fed bird.

Fig. 6a. Transitional feather of thyroidectomised bird.

6b. Normal transitional feather.

Fig. 7a. Back feather of thyroidectomised bird.

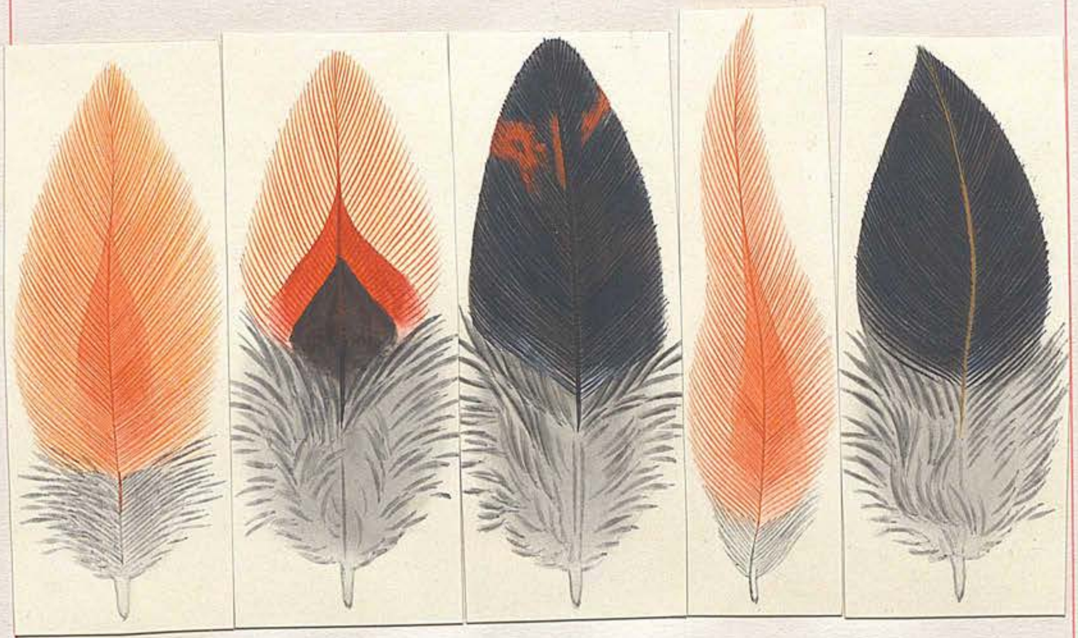
7b. Normal back feather.

7c. Back feather of thyroid fed bird.

Fig. 8a. Wing bar feather of thyroidectomised bird.

8b. Normal wing bar feather.

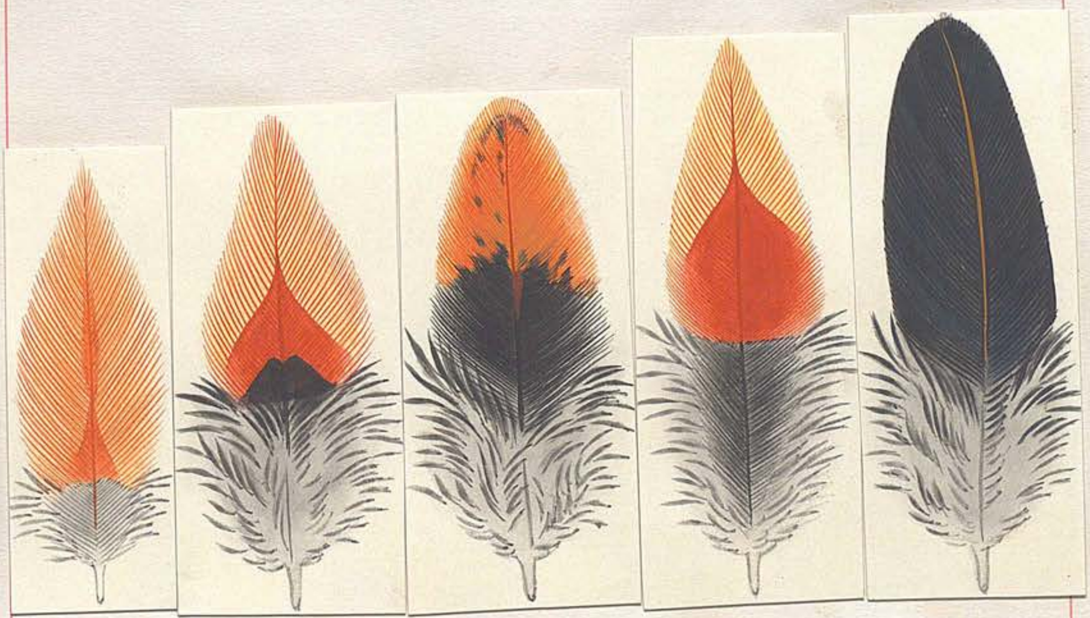
# Plate II



5a 5b 5c 6a 6b

Cape

Transitional (between neck & cape)



7a 7b 7c 8a 8b

Back

Wing bar

Plate III.

Fig. 9a. Saddle feather of thyroidectomised bird.

9b. Normal saddle feather.

9c. Saddle feather of thyroid fed bird.

Fig. 10a. Neck hackle of thyroidectomised bird.

10b. Normal neck hackle.

10c. Neck hackle of thyroid fed bird.

# Plate III

9a 9b 9c

Saddle

10a 10b 10c

Neck hackle

Plate IV.

Fig. 1. Wing bow feather of thyroid fed bird(adult) ( 240 mg./day ).

1'. Wing bow juvenile feather of second generation.

Fig. 2. Wing bow feather of thyroid fed bird(adult) ( 160 mg./day ).

2'. Wing bow juvenile feather of third generation.

Fig. 3. Shoulder feather of thyroid fed bird(adult) ( 240 mg./day ).

3'. Shoulder juvenile feather of first generation.

Fig. 4. Shoulder feather of thyroid fed bird(adult) ( 160 mg./day ).

4'. Shoulder juvenile feather of third generation.

Fig. 5. Cape feather of thyroid fed bird ( 240 mg./day ).(adult).

5'. Cape juvenile feather of second generation.

Fig. 6. Cape feather of thyroid fed bird ( 160 mg./day ).(adult).

6'. Cape juvenile feather of third generation.

Plate IV

Plate V.

Fig. 7. Back feather of thyroid fed bird ( 240 mg./ day ).(adult).

7'. Back juvenile feather of second generation.

Fig. 8. Back feather of thyroid fed bird ( I60 mg./ day ).(adult).

8'. Back juvenile feather of third generation.

Fig. 9. Saddle feather of thyroid fed bird ( 240mg./ day ).(adult).

9'. Saddle juvenile feather of third generation.

Plate V

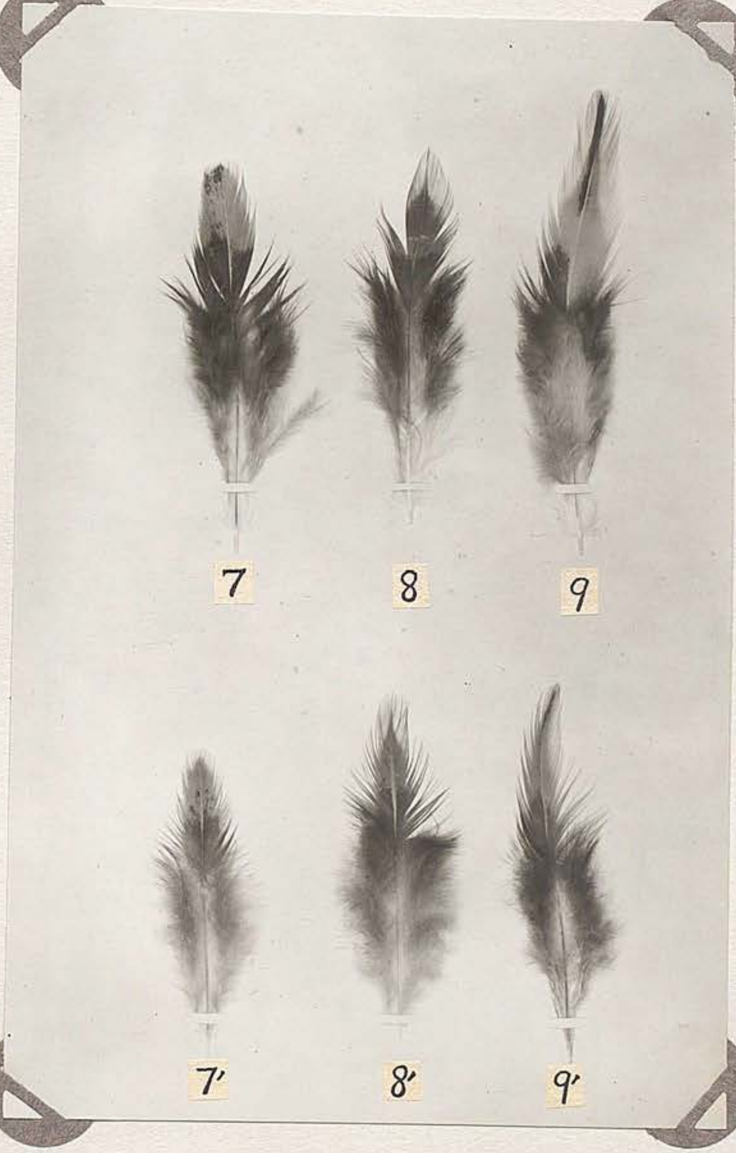


Plate VI.

Fig. IO. Shoulder feather induced by thyroid feeding in the thyroidectomised juvenile chick.

IO'. Shoulder feather of the adult cock.

Fig. II. Induced wing bow feather in the juvenile chick.

II'. Wing bow feather of the adult cock.

Fig. I2. Induced back feather in the juvenile chick.

I2'. Back feather of the adult cock.

Fig. I3. Induced saddle feather in the juvenile chick.

I3'. Saddle feather of the adult cock.

Plate VI

## IV. Acknowledgement

The writer is greatly indebted to Prof. F. A. E. Crew for his scientific hospitality and encouragement; he is specially indebted to Dr. A. W. Greenwood for his constructive suggestions and criticisms during the course of study. To Dr. J. S. S. Blyth who has given the writer much valuable assistance in the preparation of this thesis he wishes to express his gratitude.

## V. General Summary and Conclusions of the Studies on the Plumage of the Brown Leghorn Male.

Apart from the tips of a few wing flight feathers the entire feathering of the newly hatched chick consists of down. This is structurally similar on all regions, but the colour differences exhibited result in a characteristic pattern. This is quite unrelated to the regional pattern developed in the adult bird.

The replacement of down by definitive chick feathers, begins immediately and is initiated in the different body regions in a definite sequence. Within these regions a constant order of emergence also obtains. Before the down has been completely replaced chick feathering gives way to the juvenile type and this appears in a continuance of the serial order until the pterylae have developed their full complement of feathers. After /

After this moulting of the chick feathers and their replacement by juvenile ones begins, generally in the same orderly manner.

The chick plumage is characterised by a black and drab colouration, and the full development of barbules along the barbs (except in the feathers of the thigh where semiplumes are present). The red pigmentation, typically exhibited in the feathers of both juvenile and adult males, is never visible at this stage.

The onset of juvenile feathering is first visible at about six weeks of age; this phase, arbitrarily defined to include all feather types between the chick plumage and the adult form, comprises a varying number of generations due to variations in moulting rate and the seriation of feather replacement. The generations do not form /

form discrete types but represent intermediate points in the continuous gradually changing character of the feathers between first juvenile and adult plumage.

The feathers of this group are characterised by a black and red pigmentation, and by the gradual appearance of fringing in some regions in successive generations. The proportion of melanin, at first extremely high, becomes progressively reduced as maturity is approached. Variations in the degree to which these changes occur in the different regions of the body lead to the assumption of distinctive feather types in the various areas. This regionalisation also becomes more pronounced with age.

Consideration of these phenomena led to the conclusion that either (1) some stimulus influencing feather morphology was undergoing a /

a progressive change throughout the immature life of the bird, or (2) there was a continuous alteration in feather response to a constant stimulus.

From the reports of earlier workers it appeared possible that the thyroid hormone was the stimulus involved, and a histological study of this gland in growing chicks at various ages disclosed appearances which have been interpreted as indicating a decreasing activity between the ages of 8 weeks and maturity. This is in line with a suggestion made that the juvenile plumage reflected a decreasing level of thyroid activity.

In order to investigate this question further a series of experiments on thyroidectomy and thyroid feeding were undertaken.

In juvenile and adult males thyroidectomy tends to reduce the contour feathers to a uniform type /

type of red barbuleless feathers with pointed tips. The number of feather barbs is also decreased, and the time required for completion of growth greatly prolonged. The non-viability of thyroidectomised baby chicks rendered impossible the determination of the effect of the operation on the first definitive plumage.

Thyroid administration caused no change in the first definitive plumage or in the first generation of juvenile plumage. In the second and third juvenile stages feathers similar to the first generation resulted. In the adult,plumage developed following this treatment, was also juvenile in type: the tendency was towards a black unfringed type of feathering; the number of barbs per feather appeared unaltered but feather growth was completed more rapidly than normal.

By /

By administration of graded doses of thyroid substance it was possible to reproduce in mature cocks plumages resembling those of the second and third juvenile generation. Similar treatment of six-week old males which had previously had their thyroid glands removed resulted in the exhibition of plumage of the adult type.

The results support the hypothesis that that sequence of juvenile and adult feather types exhibited by the growing male express a gradually lessening degree of hyperthyroidism, due to a gradual decrease in the level of thyroid activity or to a changing response in the feathers. It is uncertain from the experiments whether the first definitive plumage fits into this series, or whether thyroid is involved at all in its expression

The variations in feather reaction in the different body regions are consistent with the view of earlier workers that they represent varying degrees /

degrees of response to thyroid. An attempt to correlate them with the relative rates of feather growth in these regions proved abortive.

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